

1 SUBMITTED TO: BIOLOGICAL INVASIONS

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4 **The complex interaction network among multiple invasive bird species**  
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6 **in a cavity-nesting community**  
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60 Running title: Interaction network among invasive birds  
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## 27 **Summary**

1 28 Alien invasive species have detrimental effects on invaded communities. Aliens do not invade  
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4 29 a vacuum, but rather a community consisting of native and often other alien species. Our  
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6 30 current understanding of the pathways and network of interactions among multiple invasive  
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9 31 species within whole communities is limited. Eradication efforts often focus on a single target  
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11 32 species, potentially leading to unexpected outcomes on interacting non-target species. We  
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14 33 aimed to examine the interaction network in a cavity-nesting community consisting of native  
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16 34 and invasive birds. We studied the cavities in the largest urban park in Israel over two breeding  
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19 35 seasons. We found evidence for a complex interaction network that includes negative, neutral  
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21 36 and positive interactions, but no synergistic interactions among aliens. Three major factors  
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23 37 shaped the interaction network: breeding timing, nesting preferences and the ability to excavate  
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26 38 or widen the cavities, which were found to be a limited resource. Cavity enlargement by the  
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28 39 early-breeding invasive rose-ringed parakeet allows breeding of the invasive common myna in  
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31 40 previously unavailable holes, likely enhancing myna establishment. The myna excludes the  
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33 41 smaller invasive vinous-breasted starling, a direct competitor of the primary nest excavator, the  
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36 42 native Syrian woodpecker. Therefore, management and eradication efforts directed towards the  
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38 43 common myna alone may actually release the vinous-breasted starling from competitive  
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41 44 exclusion by the myna, increasing the negative impact of the vinous-breasted starling on the  
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43 45 native community. As found here, interactions among multiple alien species can be crucial in  
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45 46 shaping invasion success and should be carefully considered when aiming to effectively  
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48 47 manage invasive species.

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50 48  
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52 49 **Keywords:** Biological invasions, cavity-nesting community, cavity network, common myna,  
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55 50 invasive birds, multiple species, urban park.

51 **INTRODUCTION**

1 52 Introductions of non-native species into an ecosystem can lead to detrimental effects on the  
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4 53 environment (Clavero and Garcia-Berthou 2005, Mack et al. 2000). They also offer an  
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6 54 opportunity to test fundamental theory and basic ecological processes shaping the  
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9 55 establishment and spread of introduced species in new ecosystems (Lodge 1993, Sax et al.  
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11 56 2007). The establishment success of an alien species and its impacts (Shirley and Kark 2009)  
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14 57 are affected not only by its own traits and preferences but also by those of the species already  
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16 58 found in the invaded community (Elton 1958, Levine et al. 2004, Richardson 2004, Simberloff  
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18 59 2006, Stohlgren et al. 2003), and particularly by other alien species (Ruscoe et al. 2011). While  
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21 60 substantial attention has been directed in the past decade towards better understanding  
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23 61 establishment process of single species, less work has focused on the effect of the interactions  
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26 62 among multiple species in the invaded community (of alien and native species) on  
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28 63 establishment success. This is especially important as efforts to control a given species may  
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31 64 have indirect (sometimes unpredictable) effects on non-target species in the ecosystem  
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33 65 (Courchamp et al. 1999, 2000, 2003; Crooks and Tompkins and Veltman 2006; Caut et al.  
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35  
36 66 2009; Ruscoe et al. 2011). These may actually lead to additional negative impacts of the  
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38 67 remaining untreated alien species on the native community (Soule et al. 1988; Palomares et al.  
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40 68 1995; Crooks and Soule 1999; Zavaleta et al. 2001; Caut et al. 2007; Rayner et al. 2007; Le  
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43 69 Corre 2008; Bergstrom et al. 2009; Ritchie and Johnson 2009, Ruscoe et al. 2011).

45 70 For instance, the removal of apex predators or strong alien competitors may impact  
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48 71 local communities, thus indirectly positively impacting other alien species. This may  
49  
50 72 consequentially have detrimental effects on conservation efforts (Ruscoe et al. 2011; Ritchie  
51  
52 73 and Johnson 2009). In New Zealand, the removal of invasive possums led to a significant  
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55 74 increase in the number of invasive rats (Ruscoe et al. 2011), with the release from competition  
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57 75 for food being proposed as the mechanism behind this increase (Sweetapple and Nugent 2007,  
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60 76 Ruscoe et al. 2011). Relatively little attention has been directed to empirically examine the  
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77 impacts of competition among different alien species on establishment and removal success  
78 and their interaction network (Caut et al. 2007; Trewby et al. 2008). Romanuk et al. (2009)  
79 used a simulation approach to integrate an interaction network based on species traits into  
80 invasion models. They found that that both species traits and the trophic interactions between  
81 species can influence invasion success (Romanuk et al. 2009). Thus, better understanding of  
82 the interaction network among alien species invading a single community is important for  
83 conservation efforts.

84 Empirical studies examining the interactions among alien species and their effect on  
85 establishment success have mostly focused on negative interactions, such as predation and  
86 competitive exclusion (e.g. Elton 1958, Moulton and Pimm 1983, Simberloff and Boecklen  
87 1991, Ruscoe et al. 2011). However, at least four types of interactions between individuals of  
88 different species within a community can occur, all of which may affect the invasion outcomes.  
89 The major interaction types include: negative (-/-) (e.g. aggressive behaviour following  
90 competition over a resource and affecting the fitness of individuals), positive (+/+), neutral  
91 (with no clear effect on fitness), and positive/negative (+/-) relationships, in which one species  
92 benefits from the interaction while another loses as a result of the interaction, also called  
93 contramensalism (Hodge and Arthur 1996; see table 1 in Simberloff and Von Holle 1999).  
94 Simberloff and Von Holle (1999) proposed that positive (synergistic) interactions among  
95 different alien species can be more important than previously recognized.

96 While positive interactions in plants have received attention in facilitation studies  
97 (Brooker et al. 2008, Callaway 2007, Thorpe et al. 2011), relatively little empirical work has  
98 examined the interaction network of animal communities that consist of several native and  
99 introduced species. Most studies addressing the interactions between alien species that  
100 included animals concentrated on interactions between species belonging to different trophic  
101 levels (e.g., a plant and its pollinator/dispersal agent, predators and prey or parasite and host;  
102 Grosholz 2005, Nuñez et al. 2008, Simberloff and Von Holle 1999). If we aim to predict

103 invasion results and to manage them effectively, it is essential to understand the interaction  
104 network among alien species and among the aliens and their native counterparts at a whole  
105 community level in the framework of one study (Simberloff 2006, Ruscoe et al. 2011), which  
106 was the goal of this study.

### 107 **The cavity-nesting bird community**

108 In animals, the examination of the interaction network at a whole community scale is  
109 often difficult. However, cavity-nesting birds provide a good opportunity to test such complex  
110 interactions (Aitken and Martin 2008, Blanc and Walters 2007, 2008), comprising of a clearly  
111 defined community where species potentially compete over the same resource, the nesting  
112 cavities (Martin et al. 2004, Newton 1994, but see Wesolowski 2007). In many cases, a small  
113 proportion of cavity-nesting bird species, mainly woodpeckers (*Picidae*), are the major  
114 engineers of cavities. They are thus termed primary excavators (Newton 1994, Drever et al.  
115 2008). The majority of cavity-nesting species cannot excavate their own nests. These are called  
116 secondary cavity-nesters that rely on available woodpecker-built cavities, on natural cavities  
117 generated by insects, fungal decay and other processes or on human-made cavities. Some bird  
118 species cannot excavate a cavity alone, but can enlarge or alter available cavities, especially in  
119 soft timber (Martin et al. 2004), they are called weak excavators. The variability among the  
120 cavity nesters leads to a nest web of interactions among the different cavity-nesting birds  
121 within a given community (Blanc and Walters 2007, 2008, Martin and Eadie 1999).

122 Cavity-nesting species can differ in their cavity preferences (Martin et al. 2004) and  
123 many interactions occur around the cavity resource (e.g., during selection of cavities and  
124 competition over them; Blanc and Walters 2008). For example, the cavity entrance size  
125 determines which nesting species and/or predators can enter and use the nests (Remm et al.  
126 2006, Wesolowski 2002). Moreover, cavities are often a limited resource (Albano 1992,  
127 Orchan 2007, Rendell and Robertson 1989, Van Balen et al. 1982, Wiebe 2001, but see  
128 Wesolowski 2007), especially in urban habitats, due to uprooting of decaying trees (Davies

129 2009, Newton 1994). The availability of cavities is known to determine breeding densities  
130 (e.g., Orchan 2007, Strubbe and Matthysen 2007, but see Wesolowski 2007) together with the  
131 interactions among the cavity-nesting species (Martin et al. 2004). Since many introduced bird  
132 species often tend to first establish in human-dominated areas (Chiron et al. 2009, McKinney  
133 2006), and particularly in urban parks (Case 1996), cavity availability can have much impact  
134 on the potential of alien cavity-nesting species to establish successfully (Pell and Tidemann  
135 1997, Strubbe and Matthysen 2007), and eventually on their impacts on the native community.  
136 Cavity-nesting communities are comprised of a hierarchy of users that interact both directly  
137 and indirectly (Blanc and Walters 2008).

138 In this study, we aim to study the interaction network among three alien and four native  
139 cavity-nesters during the breeding season. Following detailed field work, we construct the  
140 interaction network within the cavity-nesting bird community in an urban park, the Yarkon  
141 Park, by recording the breeding behaviour of the cavity-nesting species in the area. While this  
142 community is large enough to show complex interactions over the cavity resource, it is small  
143 enough to enable us to construct and understand the interaction network. In an earlier study, we  
144 found high percentage of natural cavity and artificial nest boxes occupation, which indicates  
145 that nesting holes are a limited resource in the study area (Orchan 2007).

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

## 155 MATERIAL AND METHODS

### 1 156 Study system

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4 157 The study was conducted in the Yarkon Park, Tel-Aviv, the largest urban park in Israel  
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6 158 (262 ha; 32°02'N, 34°47'E). The Yarkon Park comprises of several sub-environments (e.g.,  
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9 159 open lawns, a non-native Tropical Garden, Eucalyptus grove and Tamarisk grove) with a range  
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11 160 of management regimes, as detailed in Shwartz et al. (2008). Fifteen alien bird species are  
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14 161 known to have been introduced in the park, most of them since 1997 (Shwartz et al. 2008).  
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16 162 Four species have established reproducing populations of more than 150 individuals in the  
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19 163 Yarkon Park (Table 1). Of these, three alien invasive species nest in natural cavities or in  
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21 164 cavities constructed by woodpeckers (Table 1). These include the rose-ringed parakeet  
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23 165 (*Psittacula krameri*), the common myna (*Acridotheres tristis*) and the vinous-breasted starling  
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26 166 (*Sturnus burmannicus*), all originating from India/SE Asia (Table 1). The rose-ringed parakeet  
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28 167 is the only alien bird that can enlarge the cavity entrance to adjust them to its size, acting as a  
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30  
31 168 weak excavator (Kotagama and Dunnet 2007).

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33 169 We found four native species nesting in cavities in the park (Table 1). These included  
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36 170 the Syrian woodpecker (*Dendrocopos syriacus*), which is the only primary excavator in this  
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38 171 community, the Scops owl (*Otus scops*) the great tit (*Parus major*), and the house sparrow  
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41 172 (*Passer domesticus*), a native urban exploiter (Kark et al. 2007). The Syrian woodpecker  
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43 173 breeds only in cavities that it excavates and normally excavates a new cavity each year (Cramp  
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45 174 and Perrins 1994). Following the introduction of the cavity-nesting alien birds into the park,  
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48 175 the total number of bird species that use cavities almost doubled to seven species belonging to  
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50 176 six families (Table 1).

### 53 177 Cavity detection and surveillance

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56 178 Prior to the breeding season, a professional birder surveyed the study, identifying  
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58 179 potential breeding cavities were following Pell and Tidemann (1997). Their location of the  
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60 180 cavities was recorded using a GPS device. During the breeding season of 2005 (March-August)

181 and 2006 (February to August), we examined all the cavities in the field in order to identify  
182 their owner (the species nesting in each) and to record changes in cavity occupancy. We  
183 considered a species to be a cavity owner when it was seen for over two consecutive weeks in  
184 the cavity. In 2005, we visited each cavity once a week and observed the nest from the ground  
185 for 10 minutes. Occupancy was considered as a case where individuals of a given species were  
186 recorded active in the cavity or where nestlings call or eggs were seen. When necessary, in  
187 order to identify the nest owner, we climbed up to the nest using professional climbing gear.  
188 During the second study year (2006), we climbed to the cavities on a weekly basis and  
189 monitored the nests closely, using a small infra-red camera. During each visit, we identified the  
190 species nesting in the cavity and recorded evidence for breeding material, eggs, nestlings or  
191 fledglings in the nest.

192 We conducted point counts following the Distance Sampling method for population  
193 size estimates of the alien species, as detailed in Shwartz et al. 2008. For the rose-ringed  
194 parakeet, which cannot be counted reliably in the park using point counts, estimates are based  
195 on roost counts. Population size trend between 2003 and 2006 is based on our counts (Orchan  
196 2007, Shwartz et al. 2008).

### 197 **Estimating nest site characteristics**

198 In order to compare the cavity preferences among species, at the end of each breeding  
199 season, we measured 20 variables that quantify the cavity hole, cavity tree and cavity site  
200 characteristics following Newton (1994) and Martin et al. (2004). The cavity characteristics  
201 examined included: cavity depth (cavity entrance to bottom edge), cavity entrance length  
202 (height) and width, cavity entrance area (calculated as an ellipse), tunnel length, inner space  
203 diameter and cavity height above ground. We assessed the cavity age (construction year:  
204 current year, previous year or earlier) and recorded whether the cavity was excavated by the  
205 Syrian woodpecker or was generated by other decay processes. We also assessed whether the



206 rose-ringed parakeet enlarged the entrance of the cavity, as they often do in both native and  
 1 207 introduced ranges (Strubbe and Matthysen 2007) We measured the following cavity tree  
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 4 208 characteristics: circumference at cavity height, tree height (measured using a clinometer) and  
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 6 209 recorded the tree species. Site characteristics included the number of trees and number of  
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 9 210 additional cavities located in a radius of 10 m from each cavity. We also measured the distance  
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 11 211 of each cavity to the nearest cavity, its distance to the nearest permanent water source, its  
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 14 212 distance from nearest walking trail and its distance to the nearest park boundary, which also  
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 16 213 reflects the distance from built up areas. This was done using ArcGIS 9.2 (ESRI 2004).

### 20 214 **Identifying the interactions between cavity-nesting species**

22 215 We used the following cavity characteristics preferences, breeding timing and cavity  
 23  
 24 216 occupancy data to identify potential negative, positive or neutral interactions in the cavity-  
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 27 217 nesting community of the Yarkon Park.

29 218 (i) Cavity preference similarity: we first explored whether the cavity-nesting species are similar  
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 32 219 in their cavity preference using an analysis of variance (ANOVA) for the occupied cavities.

34 220 We checked for multicollinearity among the different cavity variables examined and measured.

37 221 As some variables showed significant covariation, we selected for the model the seven  
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 39 222 variables which showed the lowest autocorrelation and which we predicted will play important  
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 42 223 role in cavity selection of all species (following Paclik and Weidinger (2007); Table 2). We  
 43  
 44 224 then used a cluster analysis with an average linkage between groups (Everitt and Landau 2001)  
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 46 225 to examine similarities among the different species in their cavity characteristics (Fig. 2). Only  
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 49 226 the significant variables were included in this analysis (Table 2). We assumed that higher  
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 51 227 similarity in cavity preference may indicate stronger potential of competition and therefore can  
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 54 228 help in identifying potential negative versus neutral interaction.

56 229 (ii) Breeding timing: we explored shifts in the breeding timing of each species and the  
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 59 230 distribution of the number of nesting attempts over the breeding season. During each week of

231 the 20 weeks breeding seasons (in both 2005/6), we summed the number of nesting attempts  
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 2 232 and standardized it with the total number of nesting attempts of each species (Fig. 3) and tested  
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 4 233 the correlation among species. Significant positive correlation can indicate that two species  
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 6 234 have the same nesting timing and therefore have higher potential of competing with each other.  
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 9 235 (iii) Cavity ownership and replacement: during each of the two breeding seasons, we recorded  
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 11 236 any change in cavity ownership among the different species. We defined a “replacement” of  
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 14 237 ownership as a case where while one species showed signs of breeding activity in a given nest  
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 16 238 (e.g., nesting material, eggs or chicks), it was replaced in the same cavity during its nesting or  
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 18 239 immediately after the fledgling stage by another species. We did not consider a case as a  
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 21 240 replacement if a nest was inactive for over two weeks was later occupied by another species.  
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 23 241 Replacement while breeding was considered as a negative interaction between species.

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

### 252 **Inter-specific behavioral interactions**

253 In order to complement our understanding of the cavity preferences, we recorded the  
 254 interaction among species in the first breeding season applying dedicated behavioral  
 255 observations in the field. We examined the nest ownership dynamics at the species level, and

256 both the inter- and intra-specific behavioral interactions in the vicinity of the nest, following  
1  
2 257 Pell and Tidemann (1997). Once a week, between March and August 2005, in addition the  
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4 258 regular cavity monitoring explained above, we observed the 153 active cavities from a 50 m  
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6 259 distance for 10 minutes (after allowing a 5-min calming period upon arrival in the area). We  
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9 260 divided the interactions of individuals of one species towards another into several types:  
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11 261 negative (aggressive) interactions, positive (cooperative) and neutral interactions. Aggressive  
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14 262 interactions included distinct aggressive calls and behaviors such as directly flying at another  
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16 263 bird or when physical contact was apparent. If the attacked bird left its position, it was  
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19 264 recorded as losing the encounter. In the case of fights over cavities, we recorded the species  
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21 265 that was evicted as a loser whenever the outcome was clear (Pell and Tidemann 1997). If an  
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23 266 aggressive behaviour was recorded within the recording period, we continued watching the  
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26 267 interaction until it ceased in order to record its outcome. Neutral inter-specific interactions  
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28 268 were defined as cases where the owners of the nest and individuals of another species were  
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31 269 both near the nest, but did not act (physically or vocally) in a noticeable fashion towards each  
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33 270 other. This behavior was observed when two species nested in the close proximity, sometimes  
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36 271 in the same tree. Positive behavioral interactions near the cavity were cases where individuals  
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38 272 of different species were cooperating (e.g., joint mobbing of individuals of two different  
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40 273 species on another individual).

#### 43 274 **Data Analysis**

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46 275 All statistical analyses were performed in R software v 2.6.0 ([http://www.R-](http://www.R-project.org)  
47  
48 276 [project.org](http://www.R-project.org)). A GLM model was used to compare species hole type preference (Table 3). An  
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50  
51 277 ANOVA was used to compare mean nest preferences of species (Table 2). For both the GLM  
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53 278 and ANOVA models, we tested for compliance with model assumptions, normality and non-  
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55  
56 279 constant error variance using Kolmogorov-Smirnov and Levene's tests (Zar 1999). We used  
57  
58 280 cluster analysis (Everitt and Landau 2001) to compare species breeding preferences using the  
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60 281 estimated nest site characteristics measured. To highlight the breeding timing, a third order  
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282 polynomial relationship was fitted to the sum of active nests (per week) for each of the bird  
1 283 species studied, Pearson's correlation was used to calculate correlations between the weekly  
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4 284 sum of active nests per species.  
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## 8 285 **RESULTS**

### 10 286 **Cavity occupancy**

12 287 Over the two study seasons combined, we located a total of 290 cavities in the study  
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14  
15 288 area. After climbing up to the cavities, we found that 43 of the cavities were unsuitable for  
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17 289 nesting, being either flooded after the rain, too shallow or too small. This left a total of 247  
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20 290 cavities suitable for breeding in the area. The community of cavity-nesting bird species  
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22 291 occupied 100 woodpecker-built cavities (73% of the 137 suitable woodpecker-built cavities  
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24  
25 292 available) and 92 natural cavities (83% of the 110 suitable natural cavities recorded in the  
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27 293 study area). The cavity density in the study region was 0.7 cavities per hectare. Over the two  
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30 294 study years, we recorded 254 nesting attempts (some cavities were used multiple times over  
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32 295 the same season). Nesting attempts by alien birds were recorded in 63% of the occupied  
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35 296 cavities. Cavities with multiple breeding attempts always involved an alien bird species in at  
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37 297 least one of the attempts. Eleven trees (16%) had more than one cavity available for nesting. In  
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39 298 ten of these 11 trees, two different species bred simultaneously, and these always included the  
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41  
42 299 native urban exploiter (Kark et al. 2007) – the house sparrow (either with the common myna or  
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44 300 the rose-ringed parakeet). The number of breeding attempts in the cavities is shown in Fig. 3.  
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47 301 Surprisingly, no breeding attempt was recorded for the great tit over the whole study period  
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49 302 and only one breeding attempt was recorded for the Scops owl in our study area, which may  
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52 303 reflect the impact of the alien species in the area. We therefore excluded these two species  
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54 304 from most statistical analyses as sample size was too small but refer these finding in the  
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56 305 Discussion.  
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59 306

### 307 Nesting site characteristics

1 308 The cavity-nesting species in the Yarkon Park showed significant differences in their  
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 4 309 cavity preference and site characteristics but not in the characteristics of the breeding trees  
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 6 310 (Table 2). Based on the cluster analysis, the cavity-nesting community can be divided into  
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 9 311 three groups (Fig. 2). The first group consisted of (i) the alien vinous-breasted starling and the  
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 11 312 native Syrian woodpecker, both species used the cavities with the smallest entrance area and  
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 14 313 the lowest cavities (in terms of their location on the tree) compared with the other species  
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 16 314 (Table 2). The second group included the alien common myna and the native house sparrow,  
 17  
 18 315 both birds used the cavities with the largest entrance size (Table 2). These diverged from the  
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 20  
 21 316 thirds group, consisting of the secondary excavator – the rose-ringed parakeet. The parakeets  
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 23 317 occupied the highest and the deepest cavities of all species, generally located closer to water  
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 25  
 26 318 sources, mainly along the Yarkon River.

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 28 319 Overall, cavities were found in 11 different tree species, most of which have been  
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 31 320 planted in the urban park and are alien to the region. Cavities mainly occurred in eucalyptus  
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 33 321 (*Eucalyptus camaldulensis*; 54% of all cavities) and tamarisk (*Tamarix aphylla*; 18%) followed  
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 36 322 by the Australian she-oak (*Casuarina equisetifolia*; 9%), poplar (*Populus euphratica*; 8%) and  
 37  
 38 323 other tree species (11%). The rose-ringed parakeet showed significant preference for breeding  
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 40 324 in eucalyptus (80% of parakeet nests were in eucalyptuses,  $\chi^2=18.6$ ,  $df=4$ ,  $p<0.01$ ). The Syrian  
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 43 325 woodpecker showed significant preference for tamarisk ( $\chi^2=16.7$ ,  $df=4$ ,  $p=0.01$ ).

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 45 326 Among the natural (n=92) cavities and woodpecker-built (n=100) cavities that were  
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 48 327 occupied in the study area, 63 cavity entrances (11 natural and 52 woodpecker-built cavities)  
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 50 328 were enlarged by the rose-ringed parakeet (33%) and 122 were left intact (66%). The parakeets  
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 52  
 53 329 showed significant preference for enlarged cavities compared with un-enlarged ones in both  
 54  
 55 330 natural and woodpecker made cavities (Table 3).

56  
 57  
 58 331 The parakeets enlarged 88% of the cavities they used for breeding. The common myna  
 59  
 60 332 and the house sparrow did not show significant preference for enlarged cavities and used them

333 at a proportion of 20% for the myna compared with 33% available in the park;  $p=0.11$  and  
 334 27% for the house sparrow, (34%,  $p=0.40$ ). In contrast, the vinous-breasted starling almost  
 335 exclusively occupied intact (non-enlarged) cavities (92% of all cavities used,  $p=0.04$ ).

336 The two alien Sturnids (the common myna and the vinous-breasted starling) differed in  
 337 their cavity type preferences. While the vinous-breasted starling showed strong preference for  
 338 intact woodpecker-built cavities (Table 3), the common myna showed significant preference  
 339 for natural un-enlarged cavities (Table 3). The house sparrow did not show a statistically  
 340 significant preference for a certain cavity type (Table 3). Additionally, both the common myna  
 341 and the house sparrow used anthropogenic infrastructure for nesting (e.g., buildings and  
 342 sculptures), which were not included in the analyses here.

### 343 **Timing of the breeding season**

344 The timing of the breeding season in the park differed among some of the cavity-  
 345 nesting species (Fig. 4). The house sparrow, common myna and vinous-breasted starling  
 346 showed a peak in nest occupancy in the end of April and early May. The rose-ringed parakeet  
 347 was the first to start the breeding in February and had only a single, long breeding cycle per  
 348 pair throughout its breeding season (Fig. 4). Additionally, the rose-ringed parakeet was the  
 349 only species in which all nests were active at the same time. Its breeding season was not  
 350 strongly correlated with the other cavity-nesting species breeding in the park (house sparrow  $r=$   
 351  $-0.02$ , ns (2005), vinous breasted starling  $r = -0.38$ , ns (2005),  $r = 0.17$ , ns (2006), Syrian  
 352 woodpecker  $r = -0.28$ , ns.(2005), except for significant correlation between the nesting season  
 353 of the rose-ringed parakeet and the common myna in 2005 ( $r = -0.56$ ,  $p < 0.01$ , which was not  
 354 found in 2006 ( $r = 0.08$ , ns). The next species to start breeding following the parakeet was the  
 355 house sparrows, which had a long breeding season and with multiple breeding cycles (Table 1;  
 356 Fig. 4). Its breeding cycle was strongly correlated with the cycle of the two alien starlings in  
 357 2005 (with the common myna  $r = 0.53$ ,  $p < 0.01$ ) and with the vinous-breasted starling  $r =$   
 358  $0.73$ ,  $p < 0.00$ . It was also significantly correlated with the breeding cycle timing of the Syrian

359 woodpecker in 2005 ( $r = 0.51$ ,  $p < 0.05$ ). However, only half of sparrow breeding attempts  
 1 360 occurred simultaneously with other sparrows. The breeding cycle of the common myna was  
 2  
 3  
 4 361 strongly correlated in timing with the vinous-breasted starling ( $r = 0.80$ ,  $p < 0.001$  in 2005 and  
 5  
 6 362  $r = 0.93$ ,  $p < 0.001$  in 2006). Both Sturnids, originating from the same region, had multiple  
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 8  
 9 363 attempts over the season (Table 1) and ca. 80% of their breeding attempts occurred in the same  
 10  
 11 364 period. The breeding season of the alien common myna began three weeks earlier than the  
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 13  
 14 365 alien vinous-breasted starling. Importantly, the breeding season of the native cavity engineer,  
 15  
 16 366 the Syrian woodpeckers, coincided with all other bird species except the rose-ringed parakeet  
 17  
 18 367 ( $r = -0.28$ , ns in 2005). The peak of the breeding season of the woodpeckers in early June  
 19  
 20  
 21 368 matched that of the two alien Sturnids (Fig 4), as the early-breeding alien parakeet was  
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 23 369 approaching the end of its breeding season (only 30% of all parakeet breeding attempts  
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 25  
 26 370 occurred at that time).

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 28 371  
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 31 372 **Cavity replacements along the breeding season**  
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 33 373 Over the two study seasons, we recorded 22 replacements of cavity ownership during or  
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 35 374 immediately following the breeding cycle. The invasive common myna replaced the rose-  
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 37  
 38 375 ringed parakeet five times immediately after the parakeets ended the breeding cycle. These  
 39  
 40 376 replacements involved aggressive harassment of the nesting parakeet pairs by the common  
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 42  
 43 377 mynas during their breeding. In four of the five cases where the common myna replaced the  
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 45 378 house sparrows, the sparrows did not manage to complete their breeding cycle due to  
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 47  
 48 379 aggressive replacement by the myna. The native house sparrow replaced the rose-ringed  
 49  
 50 380 parakeet seven times by filling up the parakeet cavity with nesting material, while the rose-  
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 52  
 53 381 ringed parakeet replaced the house sparrow twice during the breeding cycle while the sparrows  
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 55 382 started bringing nesting material into the cavity. The vinous-breasted starling replaced nesting  
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 57 383 Syrian woodpeckers twice before the latter completed their breeding cycle, and replaced the  
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 59  
 60 384 locally rare Scops owl once.

### 385 Behavioral interactions among species

1 386 In the first breeding season, we conducted 1,006 behavioral observations of active  
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4 387 (occupied) cavities. In 528 occasions we recorded activity around the cavity during our  
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6 388 observations, including interactions and parental care provision for eggs and nestlings. Of  
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9 389 these, we recorded 63 inter and inter-specific interactions between cavity owners and birds of  
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11 390 other species, of which 73% (n = 46) were aggressive. Seventeen aggressive interactions  
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14 391 around the cavities (37% of all 46 aggressive interactions) were initiated by the common myna.  
15  
16 392 The vinous-breasted starling and the house sparrow initiated 18% of the aggressive interactions  
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19 393 (7) each and the rose-ringed parakeet initiated 11% (9 interactions). In all cases where we  
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21 394 recorded common mynas initiating aggressive behaviour towards the native house sparrows,  
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23 395 the sparrows eventually abandoned their nest before completing their breeding cycle (n=4).  
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25  
26 396 Eleven of the common myna interactions recorded included attacks on rose-ringed parakeets in  
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28 397 their cavities while the parakeets had either eggs or nestlings in the nest. Of the seven  
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30  
31 398 interactions involving the vinous-breasted starling, five were with Syrian woodpeckers in their  
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33 399 nests. In two of these cavities the vinous-breasted starling replaced the Syrian woodpecker  
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36 400 within less than a week from the interaction day. The interactions between the vinous-breasted  
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38 401 starling and the Syrian woodpecker and between the vinous-breasted starling and the common  
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41 402 myna were especially aggressive and included much physical contact between the interacting  
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43 403 birds. Interestingly, we did not spot any aggressive interactions between cavities owners of  
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45 404 different species in trees which had two or more simultaneous breeding attempts in different  
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48 405 cavities on the same tree. We reported this as cases of neutral interactions. We did not record  
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50 406 positive behavioral interactions between different species around the nesting sites.  
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### 55 408 DISCUSSION

57 409 Understanding the interactions among multiple alien and native species is important for  
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60 410 effectively prioritizing future conservation and control efforts and resources for mitigating  
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411 invasive species impacts (Ruscoe et al. 2011). Among birds belonging to the cavity-nesting  
1 412 community of the Yarkon Park, we found evidence for a complex network of interactions.  
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4 413 These interactions operate between native and alien species as well as among different alien  
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6 414 species. The majority of the interactions among species that have partly overlapping breeding  
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9 415 preferences were negative (Table 2, Table 3 and Fig. 2). Neutral interactions were seen among  
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11 416 species with varying nest site preferences (Fig 2) and/or with unparalleled breeding seasons  
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14 417 (Table 4, Fig. 4), such as the common myna and the Syrian woodpecker. Contramensalism (+/-  
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16 418 ) occurred where woodpeckers facilitated the breeding conditions of secondary cavity nesters  
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19 419 species and especially that of the vinous breasted starling and the rose-ringed parakeet (Fig. 3).

21 420         The most complex interactions occurred between common myna and the rose-ringed  
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23 421 parakeet, which co-occur sympatrically in native India and South East Asia. This involved both  
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26 422 negative and positive influences. The two species showed aggressive behavioral interactions  
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28 423 around active breeding cavities. This negative interaction was characterized by negative  
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31 424 interactions ("fights") over cavities, a behaviour which was also observed in their native range  
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33 425 (Dhanda and Dhindsa 1996). Sixty five percent of the aggressive interactions initiated by the  
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36 426 common myna in our observations were against rose-ringed parakeets. However, the common  
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38 427 myna benefited from the secondary excavator (the rose-ringed parakeet) by the using holes that  
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41 428 were widened by parakeets. While the mynas did not show statistically significant preference  
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43 429 to the widened cavities (possibly due to low power resulting from relatively small sample  
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45 430 sizes) availability of cavities that were suitable for mynas apparently increased due to the  
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48 431 enlargement of small entry cavities by parakeets, which were otherwise not accessible to  
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50 432 common myna, probably being too small to enter (Dhanda and Dhindsa 1996). This may be  
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52  
53 433 important as cavity nests seem to be a highly limited resource in the park, as discussed below.  
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55 434 While the widened cavities were often occupied early in the season by the parakeets, making  
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58 435 them unavailable for the myna, we found that indeed, more than half of cavities that were used  
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60 436 consecutively in the same season (5 of 9) were cases where the common myna replaced the  
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437 parakeet after the parakeet completed its breeding. We hypothesize that the ability of parakeets  
1  
2 438 to occupy the cavities earlier in the season and to protect them later (Dhanda and Dhindsa  
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4 439 1996, Pithon and Dytham 1999, Shirihai 1996) can explain these findings. In the Yarkon park,  
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6 440 mynas may partly overcome the constrains imposed by the parakeets as they are generalists  
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9 441 and can use a wider range of cavities (Dhanda and Dhindsa 1996, Feare and Craig 1999) and  
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11 442 thus successfully establish breeding populations and expand their range. Indeed, since the first  
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14 443 common myna was observed in Israel in 1997 in the Yarkon Park, the species has expanded its  
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16 444 range (Holzapfel et al. 2006) and is currently found in vast areas of Israel from the Upper  
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18 445 Galilee in the north to Eilat in the south.

21 446           Although parakeets mostly nested in woodpeckers cavities, we did not found strong  
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23 447 interspecific interaction among rose-ringed parakeets and Syrian woodpeckers. While  
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26 448 parakeets can enlarge and use woodpecker-built cavities, parakeet and woodpeckers differ in  
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28 449 their cavity type preference (Table 2, Fig. 2) and their breeding seasons only partly overlap,  
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30  
31 450 with the parakeets beginning their breeding earlier in the season than the woodpeckers (Fig. 4).  
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33 451 We also did not record any aggressive interactions or replacements between these two species.  
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36 452 Evidence from populations of parakeets in Europe reveals that parakeets enlarge the cavities  
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38 453 during three years before using them (Shwartz, A. and Strubbe, D., unpublished data). The  
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41 454 parakeet cannot use the woodpecker cavity for nesting during the first season because its  
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43 455 entrance or interior size is too small for parakeet size (Cramp and Perrins 1994, Shirihai 1994,  
44  
45 456 Feare and Craig 1999). Over the following year the rose-ringed parakeet starts its breeding  
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48 457 before the woodpecker, and extensively enlarges the entrance size of the woodpecker cavity.  
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50 458 This time delay between cavity excavation and enlargement may lead to this neutral  
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53 459 interaction.

55 460           Since there is a lag in time between the excavation process by the woodpecker and the  
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58 461 breeding of the parakeet, and since various woodpeckers excavate new breeding cavities  
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60 462 annually and prefer to nest in newly build cavities (Wiebe et al. 2007), we suggest that while  
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463 the woodpecker positively influences the parakeets the reverse interaction seems to be neutral.

1  
2 464 This finding from Israel is in agreement with work in Belgium, which did not find strong  
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4 465 influence of rose-ringed parakeets on native cavity-nesting birds (Strubbe and Matthysen  
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6 466 2007).

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9 467 Interestingly, the interaction between the aggressive common myna and the Syrian  
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11 468 woodpecker also seems to be neutral. We did not observe any aggressive interactions or  
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14 469 disturbance by mynas of woodpeckers around the cavities and did not record any cavity  
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16 470 replacements among the two species. This is likely related to the fact that the common myna is  
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19 471 too big to enter the woodpecker cavity before enlargement and cannot enlarge the cavity by  
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21 472 itself. This result is in contrary to the negative effect found in other studies of starlings, such as  
22  
23 473 the European starling (Fisher and Wiebe 2006, Winkler 1973, but see Koenig 2003), and the  
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25  
26 474 vinous breasted starling (in this study) on woodpeckers. In fact, the common myna seems to  
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28 475 facilitate the woodpecker breeding, due to its negative interactions with the vinous-breasted  
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31 476 starling, which negatively affects the native woodpeckers.

32  
33 477 The common myna and the vinous breasted starling demonstrated different preference  
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35  
36 478 for breeding cavities, and although we did not record any nest owner replacement between  
37  
38 479 these two Sturnids, we did record aggressive behavioral interactions among these species  
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40  
41 480 around cavities. The two species are partly sympatric in their native ranges (Feare and Craig  
42  
43 481 1999), overlap in their breeding timing and in their diet overlap (Feare and Craig 1999). In a  
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45 482 nest box experiment in the same study region in the Yarkon Park, Orchan (2007) found that  
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47  
48 483 while the nesting boxes in the central, food- and water-rich areas of the park were occupied by  
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50 484 the common myna while the vinous-breasted starlings mostly occupied nesting boxes located  
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53 485 far from the central, resource rich areas of the park. The starlings mainly nested closer the  
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55 486 periphery of the park, where breeding success was lower.

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58 487 Vinous-breasted starlings showed strong competition with the native woodpeckers over  
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60 488 cavities. Contrary to the mynas, the smaller vinous-breasted starling shares similar cavity

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489 preference with the woodpeckers (Table 2, Fig 2) and can occupy woodpecker nest without  
1 490 any modification of cavity size and type. They also strongly prefer to nest in intact  
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4 491 woodpeckers cavities (Table 3). Indeed, we found that vinous-breasted starlings and  
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6 492 woodpeckers interacted aggressively in most of the woodpecker cavities observed, and we  
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9 493 recorded two aggressive nesting woodpecker replacements by the vinous-breasted starling  
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11 494 during the woodpecker's breeding cycle. Thus, these species show contramensalism (+/-) as the  
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14 495 native Syrian woodpecker, which excavated majority of cavities used for breeding in the park,  
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16 496 clearly facilitates the establishment of the vinous-breasted starling. This suggests that the  
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19 497 vinous-breasted starlings may pose the largest threat to the native cavity engineers, since they  
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21 498 are small enough (Feare and Craig 1999, Cramp and Perrins 1994) to enter the cavity and their  
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23 499 nesting period overlaps.

25  
26 500 Even though the native house sparrow is among one of smaller sized species in the  
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28 501 cavity-nesting community of the Yarkon park, it was found to nest in relatively large cavities  
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31 502 (Table 2 and 3). The sparrows shared similar nesting preferences with the common mynas and  
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33 503 with the parakeets (Fig. 3). No negative interaction was recorded between the native sparrow  
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36 504 and woodpecker. However, sparrows and parakeets had more interactions. Sparrows replaced  
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38 505 seven pairs of parakeets immediately after the parakeet completed their breeding cycle. In two  
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41 506 occasions parakeets replaced the sparrows again before the latter started laying eggs. All  
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43 507 sparrow/parakeet replacements occurred either before or after (but not during) completing the  
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45 508 nesting cycle. Contrary to the parakeet, the common myna initiated interactions and replaced  
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48 509 sparrows during their breeding cycle, thus reducing their breeding success. The sparrows had  
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50 510 the largest bird population of all species in the study region, and most unoccupied nests in the  
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53 511 region were first occupied by sparrows, which filled the cavities with nesting material. The  
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55 512 sparrows were later replaced by the invasive common myna in many cases or to a lesser extent  
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58 513 by the rose-ringed parakeet.

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514 In this study, we did not record direct evidence for interaction of the alien species with  
1 515 two additional native species found in the area in much lower densities (Shwartz et al. 2008) –  
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3  
4 516 the cavity-nesting great tit and Scops owl. The fact that we found only one great tit nesting  
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6 517 cavities may reflect an impact of the growing population of invasive cavity-nesters in the study  
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9 518 area (as may be indicated by the replacement of the cavity-nesting Scops owl by the vinous  
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11 519 breasted starlings). Point counts that we conducted in the study area between 2003 and 2006  
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14 520 show decline in the great tit population size and increase in abundance of house sparrows and  
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16 521 the three alien cavity-nesting species (Table 1; Shwartz et al. 2008). This trend may alter the  
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19 522 interactions and change the availability of the already limited cavity resource in the region.

21 523 Because the Syrian woodpecker population in the study area is relatively small, it is not  
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23 524 easy to reliably estimate its population trends. However, one possible future scenario is that the  
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26 525 woodpeckers will decline in the region due to the increasing cleptoparasitism (see Kappes and  
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28 526 Davis 2008) by alien cavity nesters and that a decline of this important engineer and source for  
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31 527 breeding cavities will lead to even stronger competition over cavities, and especially over  
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33 528 natural cavities. Moreover, enlargement of cavities by the parakeet may negatively affect  
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36 529 species that prefer smaller cavities (Remm et al. 2006). This may enable predators (e.g. larger  
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38 530 birds, small mammals and reptiles) and competitors such as the mynas to enter the nest more  
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40  
41 531 easily (Shwartz et al. 2009). Previous studies have proposed that common mynas can lead to a  
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43 532 decline in the breeding success of bird species (Blanvillain et al. 2003, Currie et al. 2004, Feare  
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45 533 and Craig 1999,) when they can access the nest. These negative effects found for the common  
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48 534 myna can be worse in the case of the smaller sized vinous-breasted starling. The starling  
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50 535 showed aggressive behaviour towards the woodpeckers around cavities and was the only one  
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53 536 that replaced the native engineers in their nests during or immediately after the breeding cycle.  
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55 537 Thus, the alien vinous-breasted starling can directly and indirectly influence the abundance and  
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58 538 richness of other cavity nesters (see Aitken and Martin 2008, Drever et al. 2008 for similar  
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60 539 effects among native species).

540           The results partly support our predictions that the interaction network between different  
1 541 alien species and among alien and native species are shaped by three major factors. These  
2 3  
4 542 include (a) the nesting preferences of the cavity-nesters (as shown in Table 2 and in Fig. 2); (b)  
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6 543 the ability to excavate the cavities (thus increasing the availability of this key limited resource)  
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9 544 and (c) the overlap in their timing of breeding. Substantial evidence suggests that cavities are a  
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11 545 limited resource in the study area. Of the available cavities, 77% were occupied during the  
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14 546 breeding seasons, representing a high percentage compared with data from more natural  
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16 547 environments ( Newton 1994, Van-Balen et al. 1982, Wesolowski 2007). We recorded  
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18 548 successive usage of cavities both within and among breeding seasons which indicates the  
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21 549 potential shortage of this resource (Aitken and Martin 2008). This may imply that the negative  
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23 550 interactions between species may well arise from competition over the limited breeding  
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26 551 resources and that the woodpecker, the primary excavator, facilitates the secondary cavity  
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28 552 nesters by creating or improving the available limited resource – the nesting sites.  
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### 33 554 **Management recommendations**

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control of the rose-ringed parakeet may increase the numbers of the common mynas nesting in

566 parakeet cavities just being enlarged (Table 3, Fig. 2). Our results indicate that the control of  
567 the vinous-breasted starling may be the most beneficial management action for the native  
568 cavity nesters in the Yarkon park, as it may lead to competitive release of the woodpeckers  
569 from the alien invasive starling and may improve the breeding situation for the native great tits,  
570 the house sparrows and for the Scops owls.

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

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

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**TABLE 1**

Characteristics of the cavity-nesting bird community in the Yarkon Park, Tel Aviv, Israel. Mean incubation and nestling period refers to the total number of days between first egg laying and the last nestling to leave the nest.

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 <sup>1</sup> ( <i>Psittacula krameri</i> )	Alien	Natural and woodpecker cavities, often enlarged. Same cavities reused in subsequent years.	Northern India	1	68 ( $\pm$ 9.1) (n=24)	1963	981 $\pm$ 401 Increase
Common myna <sup>2</sup> ( <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) (n=20)	1997	2,627 $\pm$ 414 Increase
Vinous-breasted starling <sup>3</sup> ( <i>Sturnus burmannicus</i> )	Alien	Cavities in trees and in eaves and roofs.	South East-Asia	2	32 ( $\pm$ 7.8) (n=6)	2000	373 $\pm$ 102 Increase
House Sparrow <sup>4</sup> ( <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) <sup>6</sup>		
Syrian woodpecker <sup>5</sup> ( <i>Dendrocopos syriacus</i> )	Native	Self-excavated tree cavities. One pair can use several nest-cavities in one season until they successfully breed.	Israel, South East-Europe and Turkey	1	35-37 (n=13) <sup>6</sup>		
Great tit <sup>5</sup> ( <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) <sup>6</sup>		



Scops owl <sup>5</sup> ( <i>Otus scops</i> )	Native	Tree cavities, buildings.	Central West Palearctic, wintering in Central Africa and South Asia	1	46-47 (n=22) <sup>6</sup>		
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12 792 <sup>1</sup> Cramp and Perrins (1994), Shirihai (1996), Shwartz et al. (2009).

13 793 <sup>2</sup> Hatzofe and Yom-Tov (2002), Holzapfel et al. (2006), Feare and Craig (1999).

15 794 <sup>3</sup> Lin (2001), Feare and Craig (1999).

16 795 <sup>4</sup> Kark et al. (2007), Cramp and Perrins (1994), Shirihai (1996).

18 796 <sup>5</sup> Cramp and Perrins (1994), Shirihai (1996).

19 797 <sup>6</sup> Shirihai (1996).

21 798 <sup>7</sup> Calculated from data collected in this study (2006).

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**TABLE 2**

Cavity, tree and nesting site preferences of cavity-nesting birds in Yarkon park, Israel (2005, 2006 seasons). 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.

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

\*p<0.05, \*\*p<0.01, \*\*\*p<0.001, NS – non-significant.

**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). Sample sizes for each species are shown in parentheses. A and B show significant preferences for the use of cavities built by the Syrian woodpecker (vs. natural cavities), preference for enlarged (vs. unenlarged) cavities, and the significance of interaction between these two variables.

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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% *** (A)	816 64 817
	Unenlarged	91% ** (A)	75% *** (A)	8% ns	24% ns	6% ns	6518
Natural cavity	Enlarged	0% ns	0% ns	11% ns	5% ns	27% *** (B)	819 17 820
	Unenlarged	0% ns	19% ns	68% *** (A)	53% * (A)	23% ns	97821

\*  $p < 0.05$ , \*\*\*  $p < 0.001$ , 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.

**Figure legends****FIGURE 1**

Hypothetical nest web structure in the Yarkon Park. Boxes represent species in the cavity-nesting bird community. Arrows represents potential relationships between the user and the source (towards which the arrow is pointed). Pictures show the three alien cavity nesters in the community (photos by A.S.).

**FIGURE 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 (2005-2006), data are in Table 1.

**FIGURE 3**

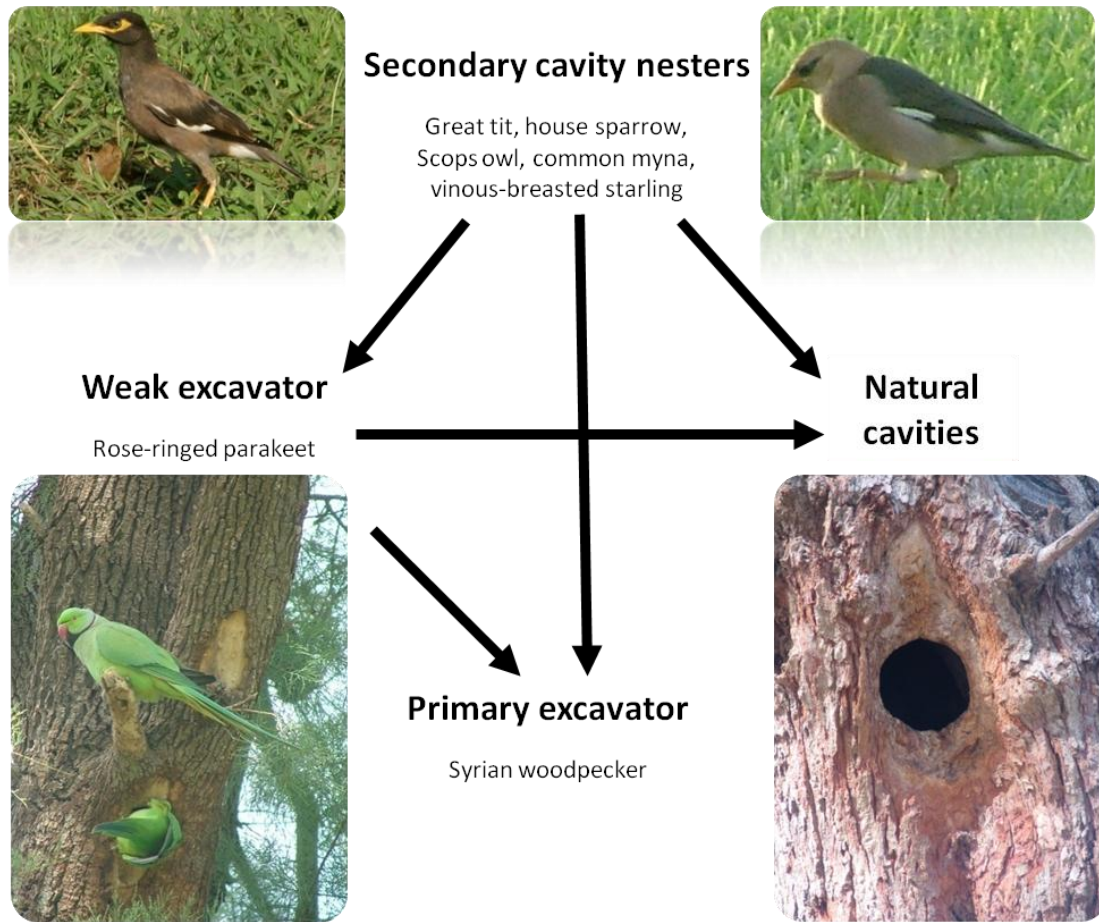
Cavity nest web diagram (following Martin and Eadie 1999) showing cavity use interactions of the native and alien (in bold) bird species of the Yarkon park. The number of nesting attempts recorded for each species is marked in parentheses. The arrows are pointed from the source of the effect towards the recipient. The proposed interaction type based on this study is marked by + (positive), 0 (neutral) and - (negative) signs following Simberloff and Von Holle (1999). 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 recipient species is not known to be affected by individuals of the source species in relation to the cavity resource. Uncertain relationships are marked with a dashed line. Arrow width represents the proportion in which each source species

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3 849 used the cavities of the recipient species ; wide arrows represent preference for the recipient cavity  
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6 850 while thin arrow indicate no-preference. For example: vinous-breasted starlings prefer  
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8 851 woodpecker cavities while common myna preferred natural cavities.  
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11 852  
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13 853 **FIGURE 4**

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15 854 Breeding timing of the cavity-nesting species of the Yarkon Park during the 2005 and 2006  
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18 855 breeding seasons. Points represent the weekly number of nesting attempts for each species and  
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20 856 lines show the corresponding relationship to the weekly number of attempts (third order  
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23 857 polynomial curve). The rose-ringed parakeet starts breeding earlier than all others. The common  
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25 858 myna and vinous-breasted starling timing fully overlaps. The Syrian woodpecker and house  
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28 859 sparrow has long breeding period and overlapped with all the aliens. Note that during the fifth  
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30 860 week almost all nests of the rose-ringed parakeet are active (hence proportion approaching 1)  
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33 861 while in the house sparrow and Syrian woodpecker only 0.5 and 0.3, respectively, of the nests are  
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35 862 active at the same time. In the common myna and vinous-breasted starling around 0.8 of the nests  
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38 863 are active at the same time.  
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**Figure 1**



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**Figure 2**

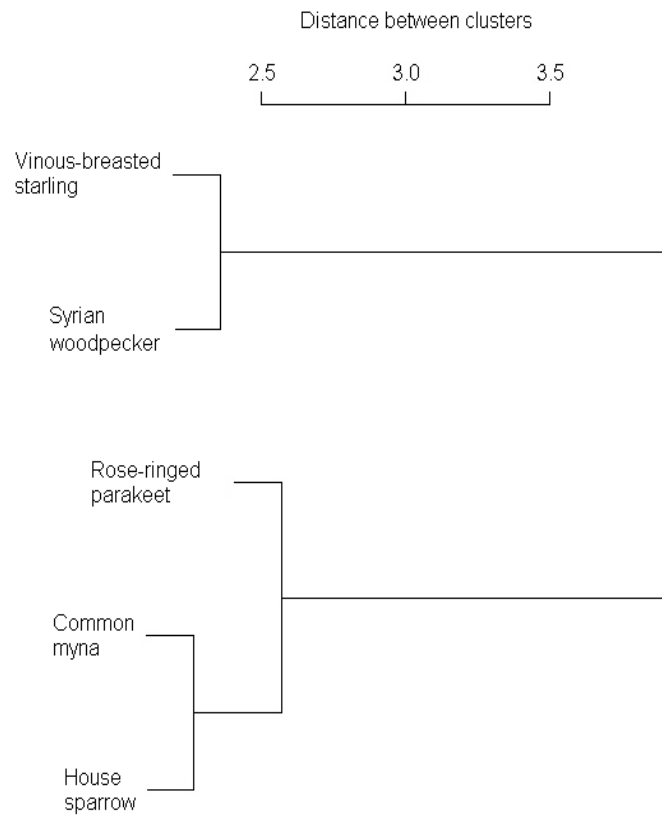
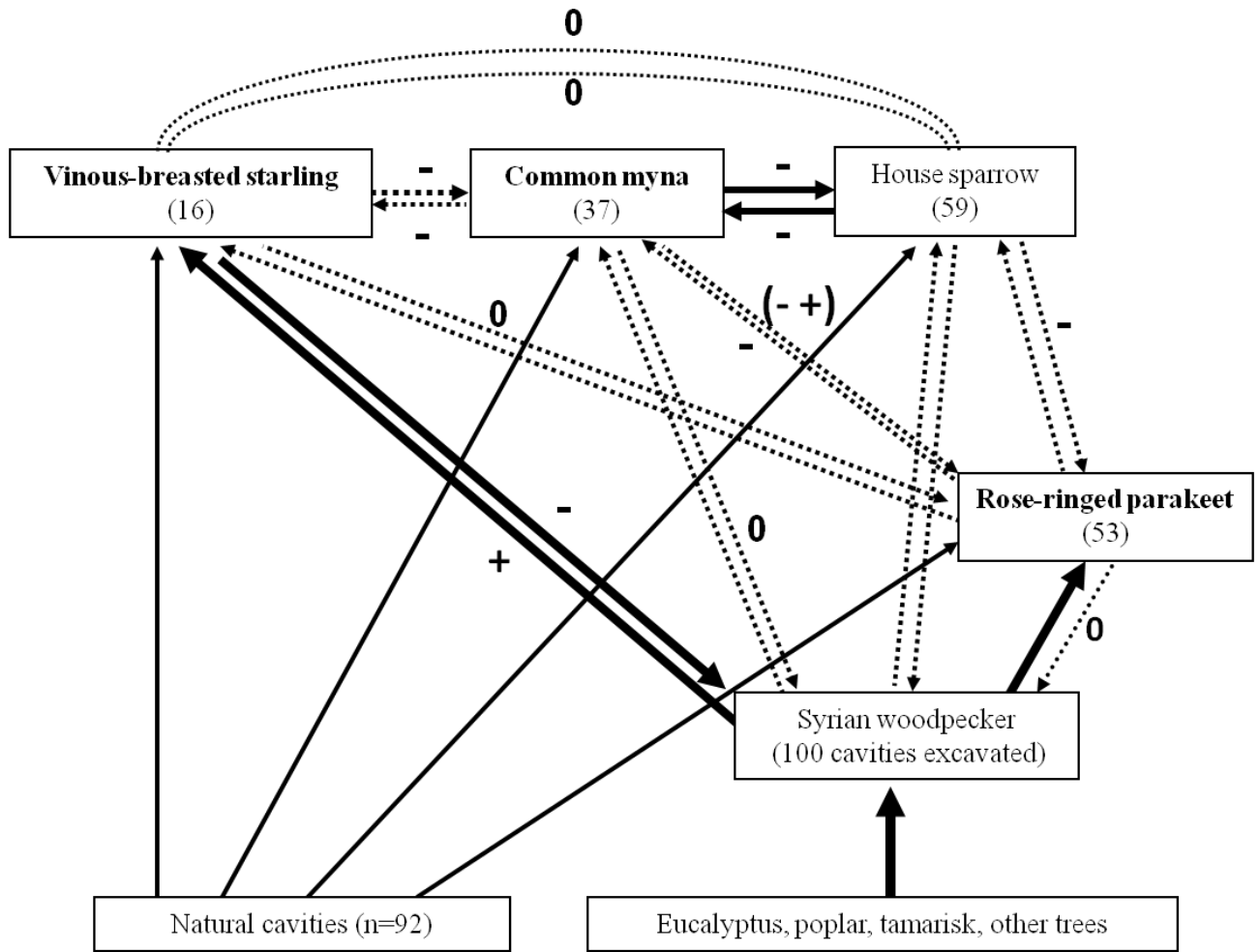


Figure 3





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**Figure 4**

