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ORIGINAL ARTICLE

Predation or facilitation? An experimental assessment of whether generalist predators affect the breeding success of passerines

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Abstract Predation has been suggested as an important factor affecting the success of breeding birds. Various studies have found that particular bird species either avoid or choose to breed in the proximity of predator nests. Here, we investigated whether the presence of a generalist predator, the Eurasian Kestrel, *Falco tinnunculus*, affects the breeding success of a passerine (House Sparrow, *Passer domesticus*), using an experimental design of nest box placement for the two species. No difference in breeding parameters was found with distance of House Sparrow nests from both active and inactive Kestrel nest boxes. However, whereas House Sparrows built nests and laid eggs in nest boxes both with and without active Kestrel nest boxes in the vicinity at a similar frequency, they laid more clutches, and the total number of eggs laid and young fledged during the breeding season was higher, in nest boxes located close to active Kestrel nest boxes than to inactive ones. Of the 367 House Sparrow nestlings banded, only 3 were found predated in Kestrel nests and no correlations were found between the percentage of birds in the Kestrels' diet and breeding parameters of the House Sparrows. The proximity of breeding Kestrels may facilitate some protection to House Sparrows from other predators, such as corvids, which are chased away by Kestrels near the nest.

Keywords Predator–prey interactions · Breeding success · Nest predation · Eurasian Kestrel · House Sparrow

Zusammenfassung Es wird angenommen, dass Prädation den Bruterfolg stark beeinflusst. Verschiedene Untersuchungen haben gezeigt, dass bestimmte Vogelarten entweder die Nähe von Nestern von Prädatoren vermeiden, oder explizit in deren direkter Umgebung brüten. In der hier vorliegenden Studie untersuchten wir. ob die Anwesenheit eines generalistischen Prädators, des Turmfalkens *Falco tinnunculus* den Bruterfolg einer Singvogelart, des Haussperlings *Passer domesticus* beeinflusst, wozu wir ein Experiment mit Nistkästen durchführten. Wir fanden keinen Unterschied in Brutparametern in Abhängigkeit von der Distanz von Sperlingsnestern zu sowohl besetzten wie unbesetzten Nistkästen von Turmfalken. Während Sperlinge mit gleicher Häufigkeit sowohl in der Nähe von aktiven wie inaktiven Nistkästen von Turmalken Nester bauten und Eier legten, hatten sie mehr Gelege, eine größere Anzahl Eier und mehr flügge Jungen in Nistkästen in der Nähe von besetzten Turmfalkennistkästen als in der Nähe unbesetzter Nistkästen. Von 367 beringten Haussperlingen wurden nur drei prädiert in Turmfalkennistkästen gefunden. Es bestand keine Korrelationen zwischen dem Anteil von Vögeln an der Ernährung der Falken und den Brutparametern der Haussperlinge. Die räumlich Nähe brütender Turmfalken könnte Haussperlinge vor anderen Prädatoren, wie zum Beispiel Rabenartige, welche von Turmfalken verjagt werden, schützen.

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Introduction

Predation has been suggested as an important factor during breeding among bird populations (Lima and Dill 1990), and it has also been suggested that prey animals may alter their reproduction and foraging behavior, as well as habitat use, in correlation with the risk of predation (Caro 2005). Very few studies have dealt with direct prey mortality, but mostly with predation risk, which has been shown to be a determinant of foraging behavior in birds (Lima and Dill 1990; Watts 1991; Lima and Valone 1991; Lima 1998; Tsurim et al. 2008, 2010), in which most birds were shown to forage near cover where predation risk is lower. Predation of birds during the breeding season may affect their breeding success (Sasvári and Hegyi 1998), with many birds prefering to breed away from potential predators in order to avoid predation (Geer 1978; Sodhi et al. 1990; Suhonen et al. 1994; Hakkarainen and Korpimäki 1996) or risk of predation (Norrdahl and Korpimäki 1998).

Other birds may choose to breed with the proximity to predator nests because of breeding facilitation (Bruno et al. 2003) or of protection from other predators (Wiklund 1982; Norrdahl et al. 1995; Blanco and Tella 1997; Bogliani et al. 1999; Bang et al. 2005). Raptors are very territorial around their nest sites and defend them against potential nest predators, mainly corvids (Paine et al. 1990; Norrdahl et al. 1995), consequently reducing the predation risk to other birds by providing safer environments with less dangerous predators. Wyrwoll (1977) found that reduced predation rate near predator nests is due to prey birds being more wary of their dangerous close neighbors than of those nesting farther away.

One of the problems of studying predator–prey interaction in birds is the difficulty of manipulating breeding birds, because many build their own nests, dwell in different habitats, and cover large territory sizes. Most studies have been observational (Wiklund 1982; Meese and Fuller 1987; Sodhi et al. 1990; Blanco and Tella 1997), although some have been able to manipulate the nest location of either the predator (Suhonen et al. 1994; Norrdahl and Korpimäki 1998; Bang et al. 2005) or the prey (Geer 1978; Norrdahl et al. 1995), but seldom both (Sasvári and Hegyi 1998; Hakkarainen and Korpimäki 1996; Morosinotto et al. 2010). The ability to manipulate both predator and prey allows researchers not only to locate the experimental system in selected habitats but also to deploy the experimental units at the spatial intervals. In observational studies, the distances between raptor nests may be large, and the habitats may therefore differ among observations due to the lack of adjacent nest sites and raptor territoriality.

Throughout their range, Eurasian Kestrels (*Falco tinnunculus*, hereafter Kestrels) are considered generalist predators with a preference for small rodents (Village 1990). Most studies of Kestrel diet in Europe revealed it to be mainly composed of small mammals (Village 1990). In comparison, Kestrel diet in Israel is more varied, and they frequently prey on birds, reptiles, and insects in addition to small mammals (Charter et al. 2007). For example, in cities in Israel, some Kestrel diets comprise close to 90% birds (Charter, unpublished data). Observational studies in Europe found that more species of birds bred far away from Kestrel nests than close to them, probably due to predation risk (Suhonen et al. 1994; Norrdahl and Korpimäki 1998). Even though Kestrels prey mainly on small mammals in Europe, the risk of predation seems to be great enough for many species to avoid breeding near Kestrel nests.

Here, we were able to employ a system in which both the potential predator (Kestrel) and prey (House Sparrow, *Passer domesticus*) breed in nest boxes and could thus be manipulated in an experimental design. In this study, we determined whether the presence of breeding Kestrels affects the occupation and breeding success of House Sparrows breeding near active or inactive Kestrel nests, and at different distances from the Kestrel nest boxes (both active and inactive). If the presence of Kestrels is perceived as a risk by House Sparrows, we would expect to find a lower occupation of sparrow nest boxes close to active Kestrel nest boxes than more distant from them. In comparison, the occupation of sparrow nest boxes located close to inactive Kestrel nest boxes should be similar regardless of the distance from the Kestrel nest boxes. If the sparrows choose to breed in proximity to Kestrels in order to obtain protection from other predators, we would expect their occupation and breeding to be higher in nest boxes closer to active than inactive Kestrel nest boxes.

Materials and methods

Study site

The study site was located in Moshav Ram On in the Jezreel Valley, Israel (32°31′55″N, 35°15′25″E), a semi-arid area lying 80–90 m above sea level. The study employed a 3-m-wide, 6-km-long path, surrounded by relatively homogenous agriculture, mainly fields of sweet corn, alfalfa, oats and wheat, grapes vines, almond plantations and olive groves.

Experimental design

The path featured 6-m-high lamp poles every 35 m. We deployed six Kestrel nest boxes (30 cm wide × 50 cm long × 30 cm high, with an entrance opening 50 cm wide × 30 cm high) and 42 sparrow nest boxes (20 cm wide × 20 cm long × 24 cm high, with a round entrance opening 5 cm in diameter). The Kestrel nest boxes were affixed at 5.5 m height and sparrow boxes at 2.5 m height to these poles, all facing east. Six groups of one Kestrel and seven sparrow boxes were deployed in the following manner: Kestrel nest boxes were attached to the light poles at intervals of 1,000 m. One sparrow nest box was placed 3 m below the Kestrel nest box and one thereafter on poles every 70 m up to a distance of 420 m. Each group of such nest boxes was separated by 420–580 m. During the 2008–2009 breeding seasons, sparrow nest boxes were visited weekly from February until the end of August, and Kestrel nest boxes at least four times during the breeding season. The Kestrel nest boxes were cleaned and moved 420 m at the end of the 2008 breeding season in September to a new location at the other side of the group of sparrow boxes in order to control for pseudoreplication. After moving all the Kestrel nest boxes to the new location, they were treated as new nest boxes. This way, no Kestrel nest box appears twice in the statistical analysis and the distance from a House Sparrow nest box to the closest Kestrel nest box differed between the 2 years. All sparrow nestlings were banded at 9–12 days old.

We recorded whether sparrow nests were built, whether eggs were laid, and whether any nestlings were fledged per breeding attempt (at least one egg laid). The date of egg-laying, clutch size, brood size (number of young after hatching) and the number of young fledged (number of young during banding at 9–12 days old minus any dead found during the visit after the young had fledged) per clutch. We calculated the following: (1) hatching success as the percentage of eggs that hatched within each clutch per breeding attempt, (2) the percentage of young that fledged from each brood per pair that hatched at least one egg, and (3) egg productivity as the percentage of eggs per nest that hatched and fledged young per breeding attempt. In Israel, House Sparrows lay up to four clutches per year (Singer and Yom-Tov 1988) and, therefore, in addition to mean clutch size and mean number of young fledged per nest box, the total number of eggs laid and the total number of young fledged during the breeding season per nest box were used as total breeding output for each nest box. Since not all of the Kestrel boxes were occupied (n = 4 in 2008) (n = 3 in 2009), the inactive boxes acted as control. Minimum distance between active Kestrel nest and control (inactive Kestrel nest box) was 1,000 m.

Pellets and remains were collected after the Kestrels had fledged. Percentage frequency of occurrence—the proportion of the total number of pellets containing a given prey item, of mammals, birds, insects and reptiles—was obtained from whole pellets only. Bands from House Sparrows were sought for in the remains.

Statistical analysis

Logistic regression was used to analyze nest-box occupation (built nest, yes/no), nest boxes in which a clutch was started (at least one egg was laid, yes/no), and nest boxes that fledged at least one young (yes/no) using the following independent variables: distance to Kestrel nest boxes, Kestrel presence or absence (0 or 1) and year. We also analyzed the effect of the distance of sparrow boxes from kestrel box on the breeding success parameters (clutch size, brood size, number of young fledged per breeding attempt, average laying date, hatching success, percentage of young fledged, and percentage egg productivity) of House Sparrows for active and inactive Kestrel nests separately, using repeated measures ANOVA (the seven nest boxes of House Sparrows beneath each kestrel were considered as dependent values). Second, after we had determined that distance did not affect any of the breeding parameters of House Sparrows, we treated the seven nest boxes as nested replicates for each Kestrel. Using a nested design ANOVA, we examined the effect of active versus inactive Kestrel nests on the breeding success parameters of House Sparrows. A t test was used to compare breeding parameters during incubation until fledging and after Kestrel young had fledged. All percentages were Arcsin square-root transformed prior to analyses. Spearman Correlations were used to analyze correlations. All tests were two-tailed. Levels of significance were set at $P < 0.05$. Statistical analyses were performed using Statistica 7.1 software and SPSS for Windows version 17.

Results

The occupation of nest boxes (built nest, yes/no) (logistic regression $P > 0.05$), nest boxes in which a clutch was started (at least one egg was laid, yes/no) (logistic regression $P > 0.05$), and nest boxes that fledged at least one young (yes/no) (logistic regression $P > 0.05$) were not significantly affected by any of the independent variables (Fig. 1).

The distance of the House Sparrow nest boxes from either active or inactive Kestrel nest boxes had no effect on any breeding success parameter of the sparrows (repeated

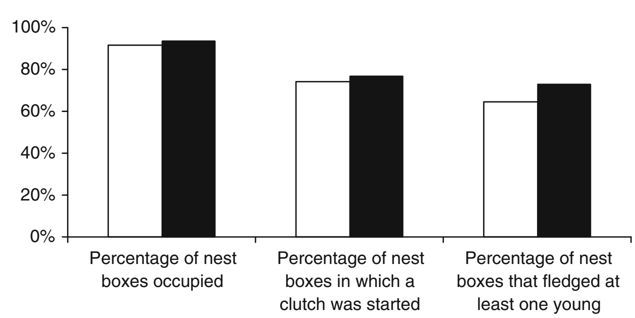

Fig. 1 Comparison between the percentage of nest boxes occupied, number of nest boxes in which a clutch was started (at least one egg was laid), and number of nest boxes that fledged at least one young in pairs of House Sparrows, *Passer domesticus*, breeding near inactive (*white*) and active (*black*) Eurasian Kestrel, *Falco tinnunculus*, nests

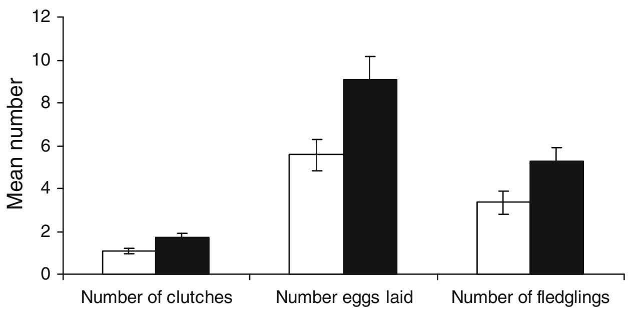

Fig. 2 Comparison between the mean total number of clutches, mean total number of eggs and mean total number of House Sparrow fledglings per nest box breeding near inactive (*white*) and active (*black*) Kestrel nests. Data are means ± SE. Statistics in Table 1

measures ANOVA, $P > 0.05$). Therefore, we treated each nest box, independent of its distance from a Kestrel box, as a replicate and used nested design ANOVA to examine the effect of Kestrel presence on the breeding success parameters of the House Sparrows. Significantly more clutches were initiated per nest box (Fig. 2), more eggs were laid (Fig. 2), and more young were fledged (Fig. 2) by sparrows breeding in nest boxes in proximity to active than to inactive Kestrel nest boxes (Table 1). Sparrow nest boxes located near active Kestrel nest boxes produced two to four clutches per nest box more frequently than sparrow nest boxes near inactive Kestrel nest boxes, which more frequently produced zero to one clutch per nest box (Fig. 3).

No differences were found when comparing sparrow breeding success during incubation + brooding periods near active Kestrel nests compared to those sparrow pairs that bred after the active Kestrel nests had fledged young, in number of eggs laid ($t_{78} = 10.33$, $P = 0.19$), number of nestlings ($t_{77} = 1.94$, $P = 0.85$), number of nestlings fledged ($t_{79} = 0.03$, $P = 0.98$), percentage of hatching success ($t_{79} = 0.83$, $P = 0.41$), percentage of fledging success ($t_{79} = 0.3$, $P = 0.71$), and the percentage of egg productivity ($t_{79} = 0.64$, $P = 0.53$).

Of the 367 sparrow young that were ringed and fledged, only 3 were found in the prey remains of Kestrels. The percentage of birds in the diet of Kestrels was not related to the number of clutches per nest box ($r = 0.07$, $n = 7$, $P = 0.88$), the number of eggs laid ($r = 0.07$, $n = 7$, $P = 0.88$), the number of nestlings fledged ($r = -0.25$, $n = 7$, $P = 0.58$), the percentage of hatching success ($r = 0.13$, $n = 7$, $P = 0.79$), the percentage of fledging success ($r = 0.022$, $n = 7$, $P = 0.64$), or the percentage of egg productivity ($r = 0.07$, $n = 7$, $P = 0.88$).

Discussion

House Sparrows built nests and laid clutches in nest boxes both with and without active Kestrel nest boxes in the vicinity at a similar frequency, but started more clutches (more breeding attempts), and therefore laid more eggs and fledged more young in nest boxes located close to active Kestrel nests than in those located near controls. The difference in total breeding output was greater in pairs breeding in nest boxes located near active Kestrel nest because those sparrows initiated more clutches; whereas the breeding output per breeding attempt was similar between pairs breeding near active or inactive Kestrel nest boxes. However, the distance from both active and inactive Kestrel nest boxes did not affect sparrow breeding parameters.

It is possible that both Kestrels and House Sparrows are affected positively by some third factor that operates independently of the powerful neighbor's protection, e.g., a possibile agricultural or landscape factor benefiting both the Kestrels via their rodent prey and the House Sparrows via easier access to more nutritious food. Although this is a possibility, because the agricultural fields surrounding the active and inactive nest boxes were very similar, we believe that any differences in reproductive parameters were unlikely to have been due to environmental differences but rather to the presence of active Kestrel nests.

The greater success of sparrows near active Kestrel nests was probably due to the protection they received from the Kestrels against other predators. Corvids, such as Hooded Crows, *Corvus corone*, and Eurasian Jays, *Garrulus glandarius*, were likely to have been the greatest predators of sparrows in this study; however, both predator species are chased away by Kestrels during the breeding season near Kestrel nests. Facilitation of breeding success through the reduction of corvid predators by raptors has been suggested elsewhere (Paine et al. 1990). In Finland, Curlews, *Numenius arquata*, bred closer to Kestrel nests than predicted and predation of their nests was found to be lower closer to Kestrel nests (Norrdahl et al. 1995), due to higher corvid predation by breeding Kestrels. In this study, the predation of Kestrels on sparrow young was very low and no correlations were found between the percentage of birds in the predators' diet and the breeding parameters of House Sparrows. It is possible that adult Kestrels (mainly males) did prey on House Sparrows that they then ate, but from the pellet analysis of prey brought back to the nest, the kill rate of young sparrows appeared to be very low. In our study, the risk of predation of sparrows by Kestrels was not high and probably lower than that by corvids.

The effect of predation risk and facilitation of breeding is probably site- and species-specific, with the same predator acting both as a facilitator and a predator (Paine et al. 1990). For example, in a study of the Fieldfare, *Turdus pilaris*, it was found that more pairs breed in proximity to Merlin, *Falco combarius*, nests (Wiklund 1982); whereas in another study, fewer of this species were found to breed

Table 1 Nested design ANOVA for the effect of the presence of active Eurasian Kestrel, *Falco tinnunculus*, nests (*Breeding Kestrels*) on several breeding success parameters of House Sparrows, *Passer domesticus*

Dependant variable	Source of variation	*df*	MS	*F*	*P*
Number of clutches	Breeding Kestrels	1	7.82	7.02	0.04
	Replicate	6	0.21	0.19	0.97
	Replicate (Kestrels)	6	1.11	0.85	0.54
	Error	69	1.31		
Total number of eggs laid	Breeding Kestrels	1	246.69	8.73	0.03
	Replicate	6	10.61	0.38	0.87
	Replicate (Kestrels)	6	28.24	0.68	0.66
	Error	69	41.31		
Total number of nestlings fledged	Breeding Kestrels	1	80.73	6.94	0.04
	Replicate	6	8.24	0.71	0.66
	Replicate (Kestrels)	6	11.59	0.75	0.61
	Error	69	15.49		
Average clutch size	Breeding Kestrels	1	5.87	4.58	0.08
	Replicate	6	0.89	0.69	0.67
	Replicate (Kestrels)	6	1.28	0.47	0.83
	Error	69	2.72		
Average number of young fledged	Breeding Kestrels	1	0.28	0.14	0.72
	Replicate	6	4.25	2.11	0.19
	Replicate (Kestrels)	6	2.02	0.57	0.75
	Error	69	3.55		
Average laying date	Breeding Kestrels	1	1,503.22	1.12	0.33
	Replicate	6	606.93	0.45	0.82
	Replicate (Kestrels)	6	1,343.85	1.67	0.15
	Error	69	804.43		
Percentage of hatching success	Breeding Kestrels	1	0.07	0.55	0.47
	Replicate	6	0.20	1.71	0.27
	Replicate (Kestrels)	6	0.12	0.36	0.90
	Error	69	0.33		
Percentage of fledgling success	Breeding Kestrels	1	0.13	0.66	0.45
	Replicate	6	0.32	1.58	0.30
	Replicate (Kestrels)	6	0.20	0.43	0.86
	Error	69	0.47		
Egg productivity	Breeding Kestrels	1	0.12	0.08	0.79
	Replicate	6	0.49	1.21	0.41
	Replicate (Kestrels)	6	0.15	0.55	0.77
	Error	69	0.28		

Replicates are the seven House Sparrow nest boxes within each Kestrel box area

close to active Merlin nests than further away (Sodhi et al. 1990).

No differences were found between breeding parameters of sparrows while Kestrels were incubating/brooding and after the Kestrel young had fledged. Even though Kestrel young do not remain in the nest box after fledgling, they do remain in the vicinity (Village 1990). At this stage, the activity of the Kestrels is at its highest, with parents not only continuing to deliver prey and protect the fledglings, but with the fledglings themselves also flying, chasing both moving (including corvids) and inert objects. It would therefore be expected that if Kestrels constituted a high predation risk to the sparrows, the latter should have shown a decrease in breeding success during the Kestrel fledgling stage. Predation, and therefore breeding success, should have been lowest when Kestrels were most active. However, since breeding facilitation and not predation seems to be the most important factor to the sparrows in our system, the continued breeding activity of the latter was probably a result of decreased corvid activity near the sparrow nest

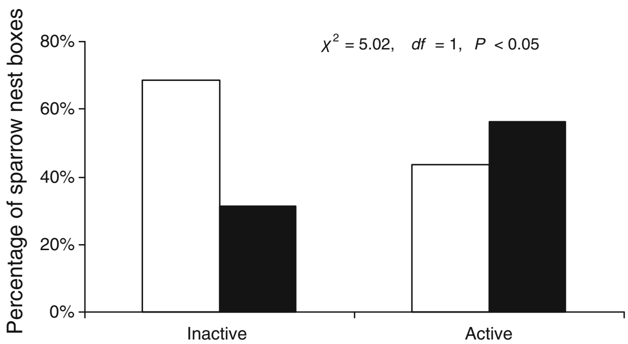

Fig. 3 Comparison between House Sparrows laying 0–1 (*white*) or 2–4 (*black*) clutches in nest boxes located near inactive or active Kestrel nest boxes

boxes, due to the former being chased away by Kestrels (both young and adults).

We did not find any difference in breeding performance of sparrows breeding at different distances from Kestrel nests. However, other studies have demonstrated in their study site that more species breed further from Kestrel nests (Suhonen et al. 1994; Norrdahl and Korpimäki 1998). The maximum distance between a Kestrel nest and the furthest sparrow nest box (420 m) was still within the Kestrel hunting territories, which may explain the lack of difference in sparrow breeding success. It is nonetheless quite remarkable that no differences were found in House Sparrows breeding on the 0-m (same pole) or 420-m nest boxes. Similar to Wyrwoll (1977), it could be that the adult House Sparrows are more wary when breeding near predators and therefore were mostly able to enter the nest boxes without predation, and that the fledglings were able to fly to sheltered areas avoiding predation by the Kestrels.

The influence and importance of breeding facilitation has been suggested to be as important as competition, predation, physical disturbance, and physiological stress in structuring communities (Bruno et al. 2003). In this study and others (Wiklund 1982; Norrdahl et al. 1995; Blanco and Tella 1997; Bogliani et al.1999; Bang et al. 2005), facilitation seems to be highly correlated to predation during the breeding season. Breeding in the proximity of predators (facilitation) or distant from them, presents two different tactics by which to avoid predation. Another possible effect of facilitation is that there may be fewer competitors for food in the presence of the breeding raptors. Different species react differently in the presence of predators, and predators react differently to different species of prey. At our study site, sparrows seem to be the dominant seed feeders, regardless of the presence of Kestrels. It is possible that species other than House Sparrows may be found in larger numbers more distant from Kestrel nests as found in other studies (Suhonen et al. 1994; Norrdahl and Korpimäki 1998), and that some of these species may compete with the sparrows for food.

The Kestrel may facilitate protection from corvids, but they themselves are still predators of sparrows. Even though the sparrows in this study bred close to Kestrel nests, this does not mean that they necessarily also foraged close to the Kestrels. If the sparrows foraged in other areas, their only close contact with Kestrel nests may have been when feeding their young. The nests were thus protected from corvids while the adults remained in minimum contact with the Kestrels. Facilitation seems to be an important factor in our experimental system, but further research comparing foraging between birds with and without the presence of Kestrels, as well as a survey monitoring other species that may compete with sparrows and prey on corvids are necessary in order to better understand how the predator–prey interaction works.

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