Israel Journal of Ecology & Evolution, 2019
http://dx.doi.org/10.1163/22244662-20191045

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Effect of supplemental feeding on nesting success in the Lesser Kestrel (*Falco naumanni*)

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Abstract The effect of food supplement to Lesser Kestrel (*Falco naumanni*) nests during the nestling period (from hatching to fledging) was studied in two nesting colonies in Israel – Alona and Jerusalem. Our hypothesis, based on diminishing returns considerations, was that food supplement will have a greater effect on fledgling success in the food-limited, urban colony of Jerusalem, than in the rural colony of Alona. Indeed, food supplement had a significantly positive effect on breeding success in both colonies. However, and contrary to our prediction, the decrease in chick mortality between supplemented and control nests in Jerusalem was not larger than in Alona (actually it was numerically smaller, albeit not significantly so). This implies either that additional factors, possibly urbanization associated, other than food limitation, might be responsible for the difference in nesting success of Lesser Kestrels between Alona and Jerusalem, and/or that the amount or the nutritional quality of the additional food provided to supplemented nests (three mice per chick per week), was not enough.

Keywords Behavioral diversity; breeding success; *Falco naumanni*; Lesser Kestrel; nest productivity; supplemental feeding; urbanization effect

Introduction

The effect of supplementary feeding during nesting has already been investigated in many studies, which mostly, but not all, demonstrated benefitting results. Focusing on small raptors, clutch size was larger and laying date was earlier for Eurasian Kestrels (*Falco tinnunculus*) which received supplemental food during pre-laying period, compared to controls (Dijkstra et al., 1982). In the same species, food supplement during the post-hatching period until fledging increased fledging number in supplemented nests, compared to controls, not only in years of low but also in years of naturally higher food supply (Wiehn and Korpimäki, 1997). Additional food provided to adult nesting Sparrowhawks (*Accipiter nisus*) during pre-laying and laying periods increased the numbers of eggs laid (Newton and Marquiss, 1981). Feeding was stopped after clutch completion, and the fed birds subsequently showed no better hatching and fledging success than did unfed birds. Food supplement increased the number of fledglings in the Burrowing Owl (*Athene cunicularia*) by 47%, relative to control nests (Wellicome et al., 2013). The increase was contributed mainly to a lesser amount of chick starvation in the treatment nests, and was less evident in years of naturally higher food supply.

The Lesser Kestrel (*Falco naumanni*) is a small falcon that breeds colonially and nests mainly in small cavities – on cliffs, on walls of abandoned quarries, under tiled roofs of rural and urban buildings, in barns and stables, or in old castles and churches (Cramp and Simmons, 1980). It is a migrating species, breeding mainly in the Mediterranean region and western and central Asia, and wintering mainly in sub-Saharan Africa. Its overall world population suffered a rapid decline during the second half of the 20^{th} century, and the species was declared as Vulnerable by the IUCN. Recent evidence, however, indicates a stable or slightly positive population trend overall during the last decade. Consequently, it was down-listed from Vulnerable and now qualifies as Least Concern (IUCN, 2018). The main cause for the past decline of the Lesser Kestrel population in its Palearctic breeding grounds has been habitat degradation, both for foraging and for nesting. Agricultural intensification and the associated land use changes, and the use of pesticides have limited and aggravated foraging areas. The abandonment and collapse of old rural buildings on one hand, and restoration works of rural and urban buildings on the other hand resulted in the loss of suitable breeding sites (Iñigo and Barov, 2011).

In Israel, where the Lesser Kestrel is a summer breeding visitor, the population trends resemble those of the global picture. According to a survey conducted in 2013, the estimated size of the Israeli breeding population was 364 pairs (Perlman, 2013), lower than the 550–600 breeding pairs estimated in a similar survey conducted in 2000 (Liven-Schulman et al., 2004), and substantially lower than

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the estimated 2000–3000 pairs breeding in Israel during the first half of the 20th century (Leshem, 1979). Thus, its conservation status, according to the 2017 edition of the Israeli Redlist (https://aves.redlist.parks.org.il, in Hebrew) was down-listed from Endangered (in the former 2002 edition) to Near Threatened.

Liven-Schulman et al. (2004) conducted observations on Lesser Kestrels in three different breeding areas in Israel: a rural colony in the Alona district, an urban colony in Jerusalem and a cliff colony in the Judean desert (open-landscape colony) about 10 km east of Jerusalem (Fig. 1). They found a significantly smaller mean fledgling number in Jerusalem, compared to the Judean desert and to Alona. They suggested that this differential success is due to factors operating during the nestling phase – the lower success in Jerusalem is caused by the relatively long flight distances between the breeding and the main hunting sites (situated more than 10 km east of Jerusalem), and the use of pesticides in the city parks and lawns. An even larger difference in mean fledgling number between Alona and Jerusalem was also reported by Bobek et al. (2018), who studied the effect of microclimatic conditions in the Lesser Kestrel nest on nest productivity in three breeding areas in Israel − Alona, Jerusalem and on the lower slopes of Mt. Gilboa (Fig. 1).

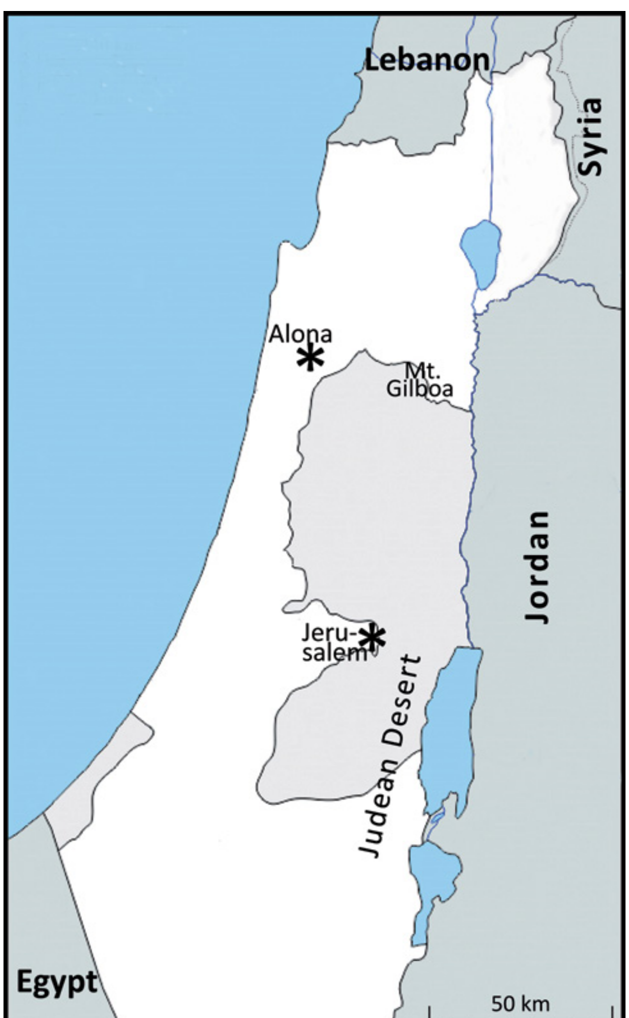

Figure 1. Map of Israel. Asterisks denote the two Lesser Kestrel colonies of our study.

In the present work, we tried to learn if food limitation during the nestling-period (i.e. from hatching to fledging) has an effect on the breeding success of Lesser Kestrels in two Israeli colonies, Alona and Jerusalem. This was done by comparing breeding success of nests that were artificially supplemented by additional food during the nestling-period, to that of control, non-supplemented nests. Moreover, considering the findings of Liven-Schulman et al. (2004) and Bobek et al. (2018), and based on the law of diminishing returns, we hypothesized that food supplement will have a greater effect on breeding success in the presumably more food-limited urban colony of Jerusalem than in the rural colony of Alona.

Methods

Study species

The Lesser Kestrel is a summer breeding visitor in Israel, arriving during the second half of February, and nesting usually terminates in early June. Clutch size is usually 3−5 eggs (Liven-Schulman et al., 2004). The estimated 2013 breeding population in Israel was 364 pairs – 63% in rural settlements, 5% in urban and 32% in the open country, mostly in quarries (Perlman, 2013). Lesser Kestrels feed almost exclusively on arthropods, mainly of the Coleoptera, Orthoptera and Solifugae orders, but also on reptiles and rodents (Kopij and Liven-Schulman, 2012).

Study area

Observations and supplementary feeding were carried out in two colonies in Israel, each representing a different breeding area (Fig. 1):

1. A rural colony in the Alona Regional Council (32°34’ N 35°01’ E, 100 m above sea level). Alona comprises of three villages, surrounded by pastures, crop fields, orchards and vineyards that are the main hunting grounds of the Lesser Kestrels, which nest mainly under roof tiles of single story buildings or in artificial wooden boxes.
2. An urban colony in the city of Jerusalem (31°47’ N 35°13’ E, 800 m above sea level). The kestrels nest under roof tiles of old, two or more story buildings, and hunt in the city parks and lawns, but mostly on the desert margins, more than 10 km east of Jerusalem.

Observations

Observations took place during 2001–2004. Infrared micro cameras (Siemens B/W AVC3086/F36) were installed in 60 nests, 37 in Alona and 23 in Jerusalem, as early as mid-February, and removed at the end of the breeding season. In each nest, a camera was placed 40–50 cm away from the eggs, which continuously recorded the situation and activity in the nest. Out of these 60 nests, 15 nests (12 in Alona and 3 in Jerusalem) failed as a result of factors not related to food shortage (e.g. eggs that did not hatch, nest predation or heat shock). The surviving nests were divided into two groups: 19 nests (10 in Alona and 9 in Jerusalem) received a supplement of food during the period from hatching to fledging, and 26 nests (15 in Alona and 11 in Jerusalem) served as controls. The supplement consisted of one thawed laboratory mouse (measuring 6 cm without the tail) per chick, placed in the evening next to the nest entrance. This was repeated three times per week, on the same days every week, until the chicks were 21 days old. The number of eggs laid, the number of eggs that hatched and the number of chicks that fledged were recorded for each nest (Table 1).

Statistical analysis

We used a generalized linear mixed model (GLMM, IBM SPSS Statistics 25) for testing the effect of Colony (Alona vs. Jerusalem) and Treatment (food supplement vs. control) on four measures of nesting success: Eggs (the number of eggs laid in the nest), Hatchlings (the number of eggs that hatched), Fledglings (the number of chicks that successfully fledged off the nest) and Chick Mortality (the number of hatchlings that did not survive). While fledgling number and chick mortality are expected to be negatively correlated, they do not necessarily arithmetically complement each other. Whereas the former measures overall nest productivity, the latter measures loss only during the nestling-period (i.e. from hatching to fledging), and can better represent the effect of food supplementation, which took place only during that period. Colony and Treatment (with Colony × Treatment interaction) were considered as fixed effects and Year as a random effect, with Poisson distributed target variables (each of the nesting success measures mentioned above).

Results

Eggs

The target variable was the number of eggs minus 3 (so that a Poisson distribution could be fitted). We found no effect of Colony ($F_{1,38} = 0.265$, $P = 0.610$) and no effect of Treatment ($F_{1,38} = 0.164$, $P = 0.688$) on the number of eggs laid in a nest, and no interaction between Colony and Treatment ($F_{1,38} = 0.507$, $P = 0.481$). Note that food supplementation started only after hatching.

Hatchlings

We found no effect of Colony ($F_{1,41} = 0.822$, $P = 0.370$) and no effect of Treatment ($F_{1,41} = 0.270$, $P = 0.606$) on the number of eggs that hatched in a nest, and no interaction between Colony and Treatment ($F_{1,41} = 0.004$, $P = 0.951$). Note that food supplementation started only after hatching.

Fledglings

Descriptive statistics are presented in Table 2. We found a significant effect of Colony on the number of chicks that successfully fledged from the nest: Alona 3.099 ± 0.414 (mean ± se), Jerusalem 1.837 ± 0.358, $F_{1,41} = 6.941$, $P = 0.012$; a significant effect of Treatment: supplement 3.213 ± 0.460, control 1.723 ± 0.313, $F_{1,41} = 8.900$, $P = 0.005$; and no interaction between Colony and Treatment: $F_{1,41} = 0.805$, $P = 0.375$.

Chick mortality

Descriptive statistics are presented in Table 2. We found a significant effect of Colony on the number of hatchlings that did not survive to fledging: Alona 0.767 ± 0.160, Jerusalem 1.465 ± 0.269, $F_{1,39} = 4.985$, $P = 0.031$; a significant effect of Treatment: supplement 0.556 ± 0.176, control 1.676 ± 0.259, $F_{1,39} = 12.840$, $P = 0.001$; and no interaction between Colony and Treatment: $F_{1,39} = 1.746$, $P = 0.194$.

Supplemented nests in Alona displayed a decrease in mortality of 1.533 ± 0.467 (mean ± se) chicks per nest (compared to control nests), whereas in Jerusalem the decrease was only 0.707 ± 0.448 chicks per nest.

Discussion

We studied two different Lesser Kestrel colonies in Israel: a rural colony in Alona district and an urban colony in Jerusalem, and found a significantly smaller fledgling success in Jerusalem than in Alona. These findings substantiate those of the studies of Liven-Schulman et al. (2004) and of Bobek et al. (2018), which were conducted in the same colonies. More specifically, Liven-Schulman et al. (2004) found a mean fledgling number per successful nest (i.e. only nests with a positive number of fledglings) of 2.44 and 1.91 for Alona and Jerusalem (respectively), and Bobek et al. (2018) found 3.16 and 1.67 for these two colonies. In the present study, also considering only the non-supplemented, successful nests, we found mean fledgling numbers of 3.56 and 1.50 for Alona and Jerusalem.

The main objective of our work was to analyze the effect of food supplement during the nestling-period (from hatching to fledging) in these two colonies. Our hypothesis, based on diminishing returns reasoning, was that food supplement would have a greater effect on fledgling success in the presumed food-limited colony of Jerusalem than in Alona. Indeed, food supplement had a significantly positive effect on nesting success – supplemented nests had a greater mean fledgling number and a smaller chick mortality. However, and *contrary* to our prediction, food supplement did not have a greater effect on fledgling success in Jerusalem than in Alona – the decrease in chick mortality between supplemented and control nests in Jerusalem was actually smaller (albeit, not significantly so) than in Alona.

This finding might suggest that additional, possibly urbanization associated factors other than food limitation, can be responsible for the difference in nesting success of Lesser Kestrels between Alona and Jerusalem. Such factors can be the use of pesticides (mainly Diazinon) against mole-crickets *Gryllotalpa gryllotalpa* in the city parks and lawns, which negatively affects kestrels' activity (Gancz et al., 2002).

Another possible factor pertains to nest microclimate. Bobek et al. (2018) demonstrated the effect of microclimate conditions on nesting success, in particular the negative

Table 1. Number of eggs, hatchlings, fledglings and dead chicks in each nest.

Year	Colony	Treatment	Eggs	No. of Chicks		
				Hatched	Fledged	Died
2001	Alona	Control	3	3	0	3
2001	Alona	Control	4	4	3	1
2001	Alona	Control	5	1	0	1
2001	Alona	Control	5	3	3	0
2001	Alona	Control	5	4	0	4
2001	Alona	Control	5	4	4	0
2001	Alona	Control	5	5	4	1
2001	Jerusalem	Supplement	N/A	3	2	1
2001	Jerusalem	Supplement	N/A	4	3	1
2001	Jerusalem	Control	5	2	2	0
2001	Jerusalem	Control	5	4	1	3
2001	Jerusalem	Control	7	3	1	2
2001	Jerusalem	Control	N/A	1	0	1
2002	Alona	Control	5	3	2	1
2002	Alona	Control	5	5	0	5
2002	Alona	Control	5	5	0	5
2002	Alona	Control	5	5	5	0
2002	Jerusalem	Supplement	4	4	3	1
2002	Jerusalem	Control	3	1	1	0
2003	Alona	Supplement	4	4	4	0
2003	Alona	Supplement	5	5	5	0
2003	Alona	Control	5	4	3	1
2003	Alona	Control	5	5	5	0
2003	Jerusalem	Supplement	5	3	2	1
2003	Jerusalem	Supplement	5	4	3	1
2003	Jerusalem	Control	4	4	2	2
2003	Jerusalem	Control	5	5	2	3
2003	Jerusalem	Control	8	3	3	0
2004	Alona	Supplement	4	2	2	0
2004	Alona	Supplement	4	3	3	0
2004	Alona	Supplement	4	3	3	0
2004	Alona	Supplement	5	4	4	0
2004	Alona	Supplement	5	4	4	0
2004	Alona	Supplement	5	5	5	0
2004	Alona	Supplement	6	5	5	0
2004	Alona	Supplement	6	5	5	0
2004	Alona	Control	4	1	0	1
2004	Alona	Control	4	3	3	0
2004	Jerusalem	Supplement	4	2	1	1
2004	Jerusalem	Supplement	4	3	3	0
2004	Jerusalem	Supplement	5	4	2	2
2004	Jerusalem	Supplement	6	4	2	2
2004	Jerusalem	Control	5	4	1	3
2004	Jerusalem	Control	5	4	1	3
2004	Jerusalem	Control	5	4	1	3

Table 2. Descriptive statistics (mean ± se) for fledging success and mortality in each Colony × Treatment combination.

		Fledged	Mortality	Decrease in Mortality (Control minus Supplement)
Alona	Supplement	4.000 ± 0.333 $n = 10$	0.000 ± 0.000 $n = 10$	1.533 ± 0.467
	Control	2.133 ± 0.506 $n = 15$	1.533 ± 0.467 $n = 15$	
Jerusalem	Supplement	2.333 ± 0.236 $n = 9$	1.111 ± 0.200 $n = 9$	0.707 ± 0.448
	Control	1.364 ± 0.244 $n = 11$	1.818 ± 0.400 $n = 11$	

effect of extensive low humidity on nest productivity. The greater success of the Alona nests was attributed to the dryer conditions within the Jerusalem nests. From Bobek (2005) data, the percent of time during which humidity within the Jerusalem nests was below a certain low threshold, was almost five times larger than within the Alona nests.

A third possibility is that the composition of the supplemented food – exclusively mice – cannot fully compensate for the chicks' nutritional requirements. Whereas mice clearly augment the chicks' diet, the lack in the supplement of the kestrels' natural food – mostly arthropods, which are less abundant in Jerusalem, but are more available in Alona – might explain the observed results. Studying pellets from under Lesser Kestrel nests in Alona and in Jerusalem during the 2002 breeding season indicated that the vast majority, in both localities, constituted of arthropod remains (Avigail Ben-Dov and Irina Levinsky, unpubl. data). Nevertheless, the difference between the two localities comes from the different feeding rates, which is smaller in Jerusalem than in Alona (Liven-Schulman et al., 2004). This is a speculation, which maybe deserves a future study that will help in planning the optimal food supplementation strategy.

Advocating the use of supplemental feeding during the nesting phase of Lesser Kestrels can gain support from many such examples. Yom-Tov (1974) reported an increased fledging success in nests of Carrion Crows (*Corvus corone*) where additional food was supplemented along the entire nesting period (including the nestling phase). Likewise, additional food supplemented during the entire nesting period (including the nestling phase) enhanced fledging success in Jackdaws (*Corvus monedula*) (Soler and Soler, 1996) and Black-billed Magpies (*Pica hudsonia*) (Dhindsa and Boag, 1989).

In addition to facilitating breeding success of target species, the negative aspects of food supplementation should not be ignored, and supplementation should be done with caution. These negative aspects include retarding the development of normal wide-range foraging behavior, altering time and energy budgets, and making birds prone to habituation to humans, which adversely affects other natural behaviors, thus restricting behavioral diversity (e.g. the California Condor *Gymnogyps californianus* – Walters et al., 2010). Plummer et al. (2013) report that winter-fed Blue Tits (*Cyanistes caeruleus*) produced offspring that weighed less, were smaller, and had lower survival. In addition, food supplementation can increase the abundance of other, non-target, species (Yarnell et al., 2014). Other negative consequences relating mainly to feeding stations can result from large aggregations of individual birds, such as the disruption of intra-guild processes and the promotion of density-dependent decreases in productivity (Cortés-Avizanda et al., 2016) or increases in infectious diseases (Blanco et al., 2011; Palomares et al., 2011; Wilcoxen et al., 2015).

While feeding kestrels near or within their nests is technically different from supplementary feeding stations, and the side effects of food supplementation may differ between species and community structures, some ecological repercussions of supplementary feeding are similar. Thus, as Moreno-Opo et al. (2015) recommend in their assessment of supplementary feeding programs for European vultures, and which is also relevant to other feeding programs, the management of supplementary feeding should be optimized from an ecological and conservation perspective, and be tailored to the specific target species needs.

Acknowledgements

We thank Bill Woodley and Igal Miller, the Society for the Protection of Nature in Israel, Israel Nature and Parks Authority and the Tisch Family Zoological Garden in Jerusalem for their help. We thank the Shulov Fund for a student's research grant (provided to A.G. by the Tisch Family Zoological Garden in Jerusalem).

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