

Effect of nest-site microclimatic conditions on nesting success in the Lesser Kestrel *Falco naumanni*

Orli Bobek^a, Adiv Gal^a, David Saltz^b and Uzi Motro ^{a,c}

^aDepartment of Ecology, Evolution and Behavior, The Hebrew University of Jerusalem, Jerusalem, Israel; ^bMitrani Department of Desert Ecology, Blaustein Institute for Desert Research, Ben Gurion University of the Negev, Sde Boker, Israel; ^cDepartment of Statistics, and The Federmann Center for the Study of Rationality, The Hebrew University of Jerusalem, Jerusalem, Israel

ABSTRACT

Capsule: Microclimatic conditions in the nests of the Lesser Kestrel *Falco naumanni*, particularly the percentage of time of extremely low humidity, affect breeding success.

Aim: To study the effect of within-nest temperature and humidity on nest productivity, and the correlation between nest productivity and the order of dates on which nests were occupied by the parents. To compare microclimatic conditions in the nest, breeding success and order of occupation between nests under tile roofs and in artificial nest boxes.

Methods: Three different Lesser Kestrel colonies were monitored in Israel – one rural, one urban and one in an open country habitat. Data loggers were placed in 39 nests for the entire breeding period to measure temperature and humidity. The number of fledglings was recorded for each nest, as well as the date of occupation.

Results: Full microclimatic data from 35 nests suggest that percentage of time of extremely low humidity is the major predictor of nest productivity – low humidity is negatively correlated with nest productivity. Sites of more successful nests were occupied earlier. Considering only successful nests, the urban colony had the lowest breeding success of the three colonies. There was no significant difference in mean productivity between nests in roofs and nest boxes, but nests in roofs were occupied earlier.

Conclusion: Nest microclimate, particularly low humidity, affects nesting success in addition to colony location.

ARTICLE HISTORY

Received 25 February 2018
Accepted 5 September 2018

Habitat selection in birds of prey is influenced by climatic conditions, the availability of appropriate prey, the presence of competitors and predators, and the availability of suitable nesting sites (Janes 1985). The optimal characteristics of a high-quality nest site are species specific, and can sometimes be deduced either by observing the rate of success of different nests or by the choices made by the birds themselves (McClaren *et al.* 2002). Cliff and cavity nesters (such as most falcon species) are among the groups that are clearly limited by the availability of nesting places (Newton 1979). Due to limitation of nesting places, some falcon species have adapted to nest in association with human dwellings – rural as well as urban – for example, the Peregrine Falcon *Falco peregrinus*, the American Kestrel *Falco sparverius*, the Eurasian Kestrel *Falco tinnunculus* and the Lesser Kestrel *Falco naumanni*.

The Lesser Kestrel 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 & Simmons 1980). It is a migrating species, breeding mainly in the Mediterranean, the Balkans and Anatolia, and in western and central Asia. It winters mostly in sub-Saharan Africa, but also a small number of adults winter in the southern part of the breeding range. The European and Asian breeding population and the wintering numbers in South Africa suffered a rapid decline from 1950, and the species was declared as Vulnerable by the International Union for Conservation of Nature (IUCN). Recent evidence, however, indicates a stable or slightly positive population trend overall during the last decade. Consequently, it was downlisted 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, primarily because of agricultural intensification and the associated land use changes and the use of pesticides. Another cause is the loss of suitable breeding sites; the abandonment and collapse of old rural buildings on one hand, and

restoration works of rural and urban buildings on the other hand (Iñigo & Barov 2011). Artificial nest boxes have been used to compensate for the loss of nest sites, especially in Europe (Pomarol 1996, Catry *et al.* 2007, Bux *et al.* 2008) and in Israel (Liven-Schulman *et al.* 2004).

Nest site characteristics and their correlation with breeding success and the frequency of use of the site have been studied for many raptor species and populations. These characteristics are usually the nest type and substrate, its location, orientation and the within-nest microclimate conditions. With reference to falcons, studies have been conducted both on natural and artificial nests.

Studying natural nests of the American Kestrel, Raphael (1985) reported that orientation influenced nest preference by the breeding kestrels, probably due to thermoregulation advantages. Studies on the use of artificial nest boxes by this species also found that the birds had a preference to particular orientations (Rohrbaugh & Yahner 1997, Butler *et al.* 2009).

Examining nest boxes of the Eurasian Kestrel in Finland, having different size and orientation, Valkama & Korpimäki (1999) found a preference to certain orientations and to intermediate nest size. Comparing the use of natural nests versus nest boxes by Eurasian Kestrels in central Spain, Fargallo *et al.* (2001) found less predation and larger productivity in nest boxes, but with increased level of infestation by parasites.

In the Lesser Kestrel, Negro & Hiraldo (1993) conducted a study of nest site occupancy and success in three colonies located in churches in southern Spain. They found that nests sites which were located high above the ground were selected by the breeders more frequently and earlier than available sites which were lower on the walls; probably to avoid predation and disturbance by predators and humans. Higher nests also realized a higher breeding success. A similar preference of higher nests was also demonstrated for Lesser Kestrels in Sicily (Sarà *et al.* 2012). Comparing artificial and natural nests of Lesser Kestrels in Portugal, Catry *et al.* (2007) found that the kestrels preferred the artificial to the natural nest sites. They concluded that installing nest boxes helped to increase the Lesser Kestrel population in Portugal. However, in Italy, Bux *et al.* (2008) showed a similar breeding success in nest boxes as in attic nests, but smaller than in natural cavities. A further study of Lesser Kestrels in Sicily by Di Maggio *et al.* (2013) demonstrated that nest type (holes versus nests under roof tiles) and orientation affected the microclimate within the nest, and consequently the hatching and fledging success.

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 the city of Jerusalem and a cliff colony in the Judean desert (open-landscape colony) about 10 km east of Jerusalem. They found a significantly smaller mean fledging rate in Jerusalem, compared to the Judean desert and to Alona. They attributed this differential success mainly to lower feeding rates in Jerusalem. The loss of hunting grounds as a result of the rapid pace of development of the city forced the adults either to hunt in sites more than 10 km east of Jerusalem or in the city parks and lawns, where the use of pesticides (mainly Diazinon) against Mole Crickets *Gryllotalpa gryllotalpa* negatively affected kestrel activity.

In the present study we examine how factors other than food limitation, such as microclimate within the Lesser Kestrel nests, had an effect on the nesting success in Israeli colonies.

Methods

The Lesser Kestrel in Israel

The Lesser Kestrel is a summer visitor to Israel, arriving during the second half of February, and nesting usually terminates in early June. They breed in colonies, both adjacent to human settlements (rural and urban) and in the open country, where they are found generally on cliffs. Clutch size is usually between 3 and 5 eggs (Iñigo & Barov 2011). The estimated breeding population in Israel is 364 pairs with 63% in rural settlements, 5% in urban areas and 32% in the open country, mostly in quarries (Perlman 2013). They feed almost exclusively on arthropods, mainly Coleoptera, Orthoptera and Solifugae orders, but also on reptiles and rodents (Gal 2006, Kopij & Liven-Schulman 2012).

Study area

Observations were carried out in three colonies, each in a different area and representing different environmental conditions: (1) in Moshav Amikam, within the Alona Regional Council (32°34'N 35°01'E, 100 m above sea level), representing a rural colony, (2) in the city of Jerusalem (31°47'N 35°13'E, 800 m above sea level), representing an urban colony and (3) on a cliff in the Revaya quarry, on the lower slopes of Mount Gilboa (32°27'N 35°27'E, 120 m above sea level), representing an open country colony.

Field sampling

In each colony, data loggers (MicroLog Temp/Hum, Fourier Systems Ltd.), that recorded temperature and

humidity every hour, were placed in several nests for the entire nesting period. The sensors were positioned inside the nest cavity, about 10 cm from the clutch. Loggers and data were retrieved only at the end of the breeding season. In Alona, some of the nests were in artificial wooden boxes, and the others were located under roof tiles. Data loggers in Alona were placed in 3 nests under roof tiles and in 4 nest boxes in 2002; in 8 nests under roof tiles and in 3 nest boxes in 2003 (out of approximately 30 nests in the colony). In Jerusalem, 5 in 2002 and 5 in 2003 (out of approximately 20 nests in the colony). In Gilboa, 5 in 2003 and 6 in 2004 (out of 8 nests on that cliff). For each of these 39 nests we recorded the date of occupation and the number of fledglings. In the Gilboa we also measured the height above ground of each nest on the colony cliff.

Statistical analysis

We used IBM SPSS Statistics (Ver. 20) for our calculations.

Two-way analysis of variance (ANOVA) was used for testing the effect of year and colony on nest productivity. For analysing the multiple effect of year, colony and microclimatic conditions in the nest on nest productivity, seven variables were considered as predictors of nest productivity (*PROD*) in a generalized linear model (GLM), with a linear scale response. Five of the variables were microclimatic variables, each measuring a possible microclimatic stress: the minimal temperature recorded in the nest throughout the nesting period (*MinTemp*), the maximum temperature (*MaxTemp*), the percentage of days which recorded a temperature above 40°C (*Temp* ≥ 40°), the percentage of days which recorded a relative humidity below 17% (*LowHum*) and the percentage of days which recorded a relative humidity above 80% (*HighHum*). The humidity thresholds were chosen as being the 5th and 95th percentiles of the humidity distribution recorded in the nests. The other two predictors, *Year* and *Colony*, were string variables. Alternative models were compared using the corrected Akaike's Information Criterion (AICc) corrected for finite sample sizes (Burnham *et al.* 2011).

The approximate occupation date of each nest was determined by direct observations on each colony. These observations took place once every three days in Jerusalem, and once every seven days in Alona and in the Gilboa, and enabled us to determine the occupation order of the nests in each colony unequivocally. In each of the six Colony × Year combinations, we ranked the nests according to the date on which they were occupied by the nesting

parents: rank 1 for the nest that was first to be occupied, rank 2 by the second, etc. Thus, we could correlate the occupation order with productivity and other nest features, using the Spearman's rank correlation analysis.

In comparing nest boxes to roof nests in Alona, two-way ANOVA was used to compare productivity, low humidity and maximal temperature, and a Mann-Whitney *U*-test was used for comparing the order of occupation between the two nest types.

When combining several different tests, each performed on a separate data set, but all testing the same null hypothesis, the overall *P* value was calculated by adding *ts* or by adding weighted *Zs* methods (Rosenthal 1978). *P* values are two-tailed.

Results

Effect of Year and Colony on nest productivity

Mean productivity per nest (i.e. the mean number of nestlings fledged per pair) are given (± se) for each of the six Year × Colony combinations in Table 1. There were no significant differences in productivity among years and no differences among colonies (two-way ANOVA, $F_{2,33} = 0.241$, $P = 0.788$ and $F_{2,33} = 1.380$, $P = 0.266$ for *Year* and *Colony*, respectively).

Considering only successful nests (Table 1, shaded column), there were still no significant differences among years, but there were significant differences among colonies (two-way ANOVA, $F_{2,18} = 0.236$, $P = 0.792$ and $F_{2,18} = 4.941$, $P = 0.019$ for *Year* and *Colony*, respectively). Tukey's *post hoc* analysis indicates significant differences both between Jerusalem and Alona ($P = 0.040$) and between Jerusalem and Gilboa ($P = 0.011$), with Jerusalem having the lower productivity in both comparisons.

Effect of microclimatic conditions in the nest on nest productivity

For analysing the effect of microclimatic conditions within the nest on nest productivity, we had complete data on 35 nests. The five microclimatic variables plus *Year* and *Colony* were considered as predictors of nest productivity (*PROD*) in a GLM. First, we checked for possible multicollinearity among the microclimatic, scale variables. Multicollinearity analysis revealed a moderate level of collinearity, which disappeared after excluding two variables: *MinTemp*, which had a negative correlation both with *MaxTemp* ($R = -0.828$, $n = 35$, $P < 0.001$) and with *Temp* ≥ 40° ($R = -0.339$, $n = 35$, $P = 0.046$), and *Temp* ≥ 40°, which had also a

Table 1. Productivity [mean \pm se (*n*)] of Lesser Kestrel nests in each of the three colonies. Each unshaded column represents a different year, whereas the rightmost column (shaded) represents mean productivity per successful nests over all years in each colony.

	2002	2003	2004	Only Successful Nests
Alona	2.571 \pm 0.719 (7)	1.727 \pm 0.524 (11)		3.157 \pm 0.311 (12)
Jerusalem	0.600 \pm 0.245 (5)	1.400 \pm 0.678 (5)		1.667 \pm 0.433 (6)
Gilboa		1.600 \pm 0.980 (5)	2.333 \pm 0.803 (6)	3.750 \pm 0.460 (6)

positive correlation with *MaxTemp* ($R = 0.556$, $n = 35$, $P = 0.001$). Checking for possible multicollinearity between the three remaining variables *MaxTemp*, *LowHum* and *HighHum*, we found variance inflation factors, $VIF = 1.112$, 1.165 and 1.101 for each predictor, respectively.

Using AICc, we thus compared between the $2^5 = 32$ possible GLMs having any subset of the five variables: *Year*, *Colony*, *MaxTemp*, *LowHum* and *HighHum* as predictors of *PROD*. Table 2 displays the 10 best fitting models, that is, those having the smaller AICc. The model with *LowHum* as a sole predictor of nest productivity was the best fitting model, and based on the evidence ratio, was better by 112% than the second best model, the one with *LowHum* and *MaxTemp* as predictors. The best model was better by 117% than the third model, with *LowHum* and *HighHum* as predictors, and better by 136% than the fourth model, with *MaxTemp* and *Colony* as predictors. Still, adhering to the suggested practice of considering all models with $\Delta AICc \leq 2$ as having similar support from the data (Burnham *et al.* 2011), we will not discard the three latter models. Each is significantly better fitted than the intercept-only model, as judged by the likelihood ratio chi-square: $\chi_1^2 = 9.419$, $P = 0.002$; $\chi_2^2 = 10.475$, $P = 0.005$; $\chi_3^2 = 10.432$, $P = 0.005$; $\chi_4^2 = 12.998$, $P = 0.005$, respectively. Nevertheless, note that *LowHum* appears in three of the four models, with a weight totalling 0.544, while the other three predictors appear at most in two of the four models with total weight being lower (*MaxTemp* = 0.252, *HighHum* = 0.130, *Colony* = 0.119).

For model averaging, we considered the three variables – *LowHum*, *MaxTemp* and *HighHum* – as predictors of *PROD* in a standardized linear regression model. The average standardized linear model,

produced by a weighted average of the $2^3 = 8$ relevant models (each weighed by its AICc weight), is $PROD = 1.831 - 0.430 \times LowHum - 0.053 \times MaxTemp + 0.050 \times HighHum$. The regression coefficients of *LowHum* and *MaxTemp* are both negative (as might have been expected), whereas that of *HighHum* is positive. Note that the standardized coefficient of *LowHum* is eight times larger than that of *MaxTemp*.

Using also a slightly different approach, in a stepwise multiple linear regression with *LowHum*, *MaxTemp* and *HighHum* as predictors of *PROD*, *LowHum* contributes 0.236 to R^2 , the addition of *MaxTemp* increases R^2 by only 0.023, and the subsequent addition of *HighHum* increases R^2 by only 0.017. *F* statistics and *P* values for each of these three respective models are: $F_{1,33} = 10.191$, $P = 0.003$; $F_{2,32} = 5.583$, $P = 0.008$; $F_{3,31} = 3.937$, $P = 0.017$. *MaxTemp* as a sole predictor of nest productivity has $R^2 = 0.083$ ($F_{1,33} = 2.994$, $P = 0.093$), and the decrease in productivity is only 0.095 chicks per 1°C increase in mean maximal temperature in the nest.

Productivity and occupation order

In each of the six Colony \times Year combinations, we calculated the correlation between nest productivity and its rank in the order of occupation (Table 3). The combined significance level was $P < 0.001$, indicating that nests that were more successful were occupied earlier.

Low humidity and occupation order

In each of the six Colony \times Year combinations, we calculated the correlation between the percentage of

Table 2. Akaike's Information Criterion corrected for finite samples (AICc) for the best 10 out of 32 GLMs. The dependent variable was nest productivity (*PROD*).

Year	Colony	Max Temp	Low Hum	High Hum	AICc	$\Delta AICc$	Akaike Weight	Evidence Ratio
			✓		134.759	0.000	0.281	
		✓	✓		136.262	1.503	0.133	2.120
			✓	✓	136.305	1.546	0.130	2.166
	✓	✓			136.474	1.715	0.119	2.357
	✓	✓	✓		137.066	2.307	0.089	3.169
		✓	✓	✓	138.174	3.415	0.051	5.515
	✓	✓		✓	139.107	4.348	0.032	8.793
✓			✓		139.848	5.089	0.022	12.737
	✓		✓		139.883	5.124	0.022	12.962
	✓	✓	✓	✓	139.988	5.229	0.021	13.660

Table 3. Spearman's rank correlation coefficients between nest fledgling numbers and the order by which nests were occupied.

Colony	Year	Number of nests	Spearman's ρ	P value
Alona	2002	7	-0.896	0.006
Alona	2003	11	-0.810	0.003
Jerusalem	2002	5	-0.577	0.308
Jerusalem	2003	5	-0.949	0.014
Gilboa	2003	5	-0.577	0.308
Gilboa	2004	6	-0.586	0.222
Combined P value				<0.001

Table 4. Spearman's rank correlation coefficients between percentage of days in which relative humidity in the nest was below 17%, and the order by which nests were occupied.

Colony	Year	Number of nests	Spearman's ρ	P value
Alona	2002	7	0.482	0.273
Alona	2003	9	0.261	0.498
Jerusalem	2002	4	0.400	0.600
Jerusalem	2003	5	0.700	0.188
Gilboa	2003	4	0.949	0.051
Gilboa	2004	6	-0.319	0.538
Combined P value				0.006

days in which relative humidity in the nest was below 17% (*LowHum*) and the order of occupation (Table 4). The combined significance level was $P = 0.006$, indicating that drier nests were occupied later.

Comparing roof nests to nest boxes in Alona

Comparing productivity between nests in roofs and nest boxes, no significant difference was found (two-way ANOVA: $F_{1,12} = 1.294$, $P = 0.278$). Percentage of days with humidity lower than 17% (which proved to be the main microclimatic predictor of nest productivity) were not different between nests in roofs and nest boxes (two-way ANOVA: $F_{1,12} = 0.039$, $P = 0.847$). Likewise, mean maximal temperatures were not significantly different between nests in roofs and nest boxes (two-way ANOVA: $F_{1,12} = 0.157$, $P = 0.699$). Yet, nests in roofs were occupied earlier than nest boxes (Mann-Whitney U-test, 2002: $U = 1.0$, $n_1 = 3$, $n_2 = 4$, $P = 0.114$; 2003: $U = 2.0$, $n_1 = 8$, $n_2 = 3$, $P = 0.048$; combined significance: $P = 0.008$).

Height above ground and reproductive success in the Gilboa colony

There was a positive correlation between the height above the ground and nest productivity (2003: $R = 0.925$, $n = 5$, $P = 0.024$; 2004: $R = 0.468$, $n = 6$, $P = 0.349$; combined significance: $P = 0.018$).

Discussion

We studied three different Lesser Kestrel colonies in Israel: a rural colony in Alona district, an urban colony

in Jerusalem, and an open country colony in the Gilboa. We found a significantly smaller mean fledgling number per successful nest in Jerusalem, compared to Gilboa and to Alona. These findings substantiate the findings of a study by Liven-Schulman *et al.* (2004), who examined Lesser Kestrel nesting success also in the rural colony of Alona and the urban colony of Jerusalem, but in a different open country colony (on a cliff in the Judean desert), several years before our study.

The main objective of our work was to correlate microclimatic conditions in the Lesser Kestrel nest to nest productivity. Microclimatic conditions evidently have an impact on the growth and survival of altricial nestlings. For instance, studying corticosterone (CORT) level in feathers of Tree Swallow *Tachycineta bicolor* nestlings, Fairhurst *et al.* (2012) demonstrated that CORT was positively correlated with increased temperature variability in the nest and maximum, but not minimum, nest temperature. While normally CORT level in Tree Swallow females did not predict the number of nestlings fledged during the same breeding season or the survival to the following season, it did predict higher survival rate of stressed females (Harris *et al.* 2017). Our study of microclimate conditions (temperature and humidity) in 35 Lesser Kestrel nests in Israel found that the main factor influencing the productivity of a nest, measured by the number of fledglings, was humidity. More specifically, the percentage of days during which humidity in a nest was below a threshold (chosen as the lower 5% of the humidity distribution in the entire 35 nests), was negatively correlated with nest productivity. Maximal temperature displayed a much weaker influence on productivity, similar to the weak influence found by Campobello *et al.* (2017), who measured nest temperature (but not humidity) in their extensive analysis of Lesser Kestrel nests in Sicily. Our study, which incorporated both the effects of temperature and humidity, indicated that dehydration was probably the main factor influencing nestling mortality. Dehydration leads to weight loss, to increased plasma osmolality and concentrations of sodium and chloride, and consequently to increased plasma concentrations of the antidiuretic hormone (AVT) and prolactin and plasma aldosterone (Arad *et al.* 1985). In extreme situations, the normal physiological pathway that mitigates these effects can break down.

Nests that fledged a larger number of young were occupied earlier by the nesting parents. A possible explanation could be that earlier occupation of nests is by more competitive and more experienced parents, which also produce more fledglings. Nesting parents

can probably perceive a priori the quality of the various nest sites, either from their own past experience or by using the breeding success of conspecifics as a source of public information (Aparicio *et al.* 2007).

Studying Lesser Kestrels in Spain, Serrano & Tella (2007) reported that violent agonistic interactions were disproportionately directed towards yearling males, which lost most aggressive encounters with older breeders when trying to settle in a colony and obtain a nest hole.

As expected from other studies (Negro & Hiraldo 1993, Sarà *et al.* 2012), also in our study the height above ground of the Gilboa nests (the only colony where height can be meaningful) and their fledgling number were positively correlated.

Studying Lesser Kestrel nesting in buildings in several towns in southern Italy, Bux *et al.* (2008) found similar occupancy rate and breeding performance of roof-top nest boxes and of under-roof nests, while nests in cavities in buildings had better (albeit, not significantly) reproductive success. The addition of artificial nest boxes contributed to an increase in the Lesser Kestrel population in Portugal (Cтры *et al.* 2007), where the kestrels even preferred the nest boxes to natural nest sites. Nevertheless, in very hot years, the high temperature and the inadequate ventilation in wooden nest boxes reached such levels that chick growth rate was reduced and chick mortality increased (Cтры *et al.* 2011). In our study, artificial nest boxes in Alona were not significantly less productive than nests under roof tiles at the same colony, and both nest types experienced similar levels of low humidity and high temperatures. Yet, nest boxes were less attractive to the kestrels, if judged by the order by which nests were occupied. One possibility is that nest boxes harbour more parasites and so are less preferred by breeding birds: Fargallo *et al.* (2001) found that Eurasian Kestrel chicks from nest boxes showed a higher intensity of infection by the ectoparasite *Carnus hemapterus* than chicks from natural nest sites.

Although microclimatic conditions in the nest affected nesting success, there are other, equally important factors, such as nest height from the ground and, moreover, colony location and human disturbance. The low nesting success in Jerusalem was attributed mainly to the lack of suitable foraging areas near the colony and to the use of pesticides in the city parks (Liven-Schulman *et al.* 2004, Gal 2006). Likewise, Sarà *et al.* (2012) and Campobello *et al.* (2017) found for the Lesser Kestrel in Sicily that among both nest and colony features, colony location and human disturbance outweighed all other predictors for the relative importance of their effect on egg and nestling survival.

Acknowledgements

We thank Tzahala Brosh, Ifat Liven-Schulman, Dan Alon, Carmel Zitronblat and the late Tirza Keren for their assistance. We thank the personnel of the Ravaya Quarry and the Israel Electric Company for help in our work on the Gilboa colony, and an anonymous reviewer for very helpful comments and suggestions. This is publication number 984 of the Mitrani Department of Desert Ecology, and number 721 of the Federmann Center for the Study of Rationality.

ORCID

Uzi Motro  <http://orcid.org/0000-0002-4761-2229>

References

- Aparicio, J.M., Bonal, R. & Muñoz, A. 2007. Experimental test on public information use in the colonial Lesser Kestrel. *Evol. Ecol.* **21**: 783–800.
- Arad, Z., Arnason, S.S., Chadwick, A. & Skadhauge, E. 1985. Osmotic and hormonal responses to heat and dehydration in the fowl. *J. Comp. Physiol. B* **155**: 227–234.
- Burnham, K.P., Anderson, D.R. & Huyvaert, K.P. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behav. Ecol. Sociobiol.* **65**: 23–35.
- Butler, M.W., Whitman, B.A. & Dufty Jr, A.M. 2009. Nest box temperature and hatching success of American Kestrels varies with nest box orientation. *Wilson J. Ornithol.* **121**: 778–782.
- Bux, M., Giglio, G. & Gustin, M. 2008. Nest box provision for lesser kestrel *Falco naumanni* populations in the Apulia region of southern Italy. *Conserv. Evidence* **5**: 58–61.
- Campobello, D., Lindström, J., Di Maggio, R. & Sarà, M. 2017. An integrated analysis of micro- and macro-habitat features as a tool to detect weather-driven constraints: a case study with cavity nesters. *PLoS ONE* **12**: e0174090. DOI: 10.1371/journal.pone.0174090.
- Cтры, I., Alcazar, R. & Henriques, I. 2007. The role of nest-site provisioning in increasing lesser kestrel *Falco naumanni* numbers in Castro Verde Special Protection Area, southern Portugal. *Conserv. Evidence* **4**: 54–57.
- Cтры, I., Franco, A.M.A. & Sutherland, W.J. 2011. Adapting conservation efforts to face climate change: modifying nest-site provisioning for lesser kestrels. *Biol. Conserv.* **144**: 1111–1119.
- Cramp, S. & Simmons, K.E.L. 1980. *Handbook of the Birds of Europe, the Middle East and North Africa – the Birds of the Western Palearctic*, Vol. 2 (Hawks to Bustards). Oxford University Press, Oxford.
- Di Maggio, R., Campobello, D., Mascara, R. & Sarà, M. 2013. Nest characteristics affect microclimate and breeding success of lesser kestrel *Falco naumanni* in the Gela plain. Proceedings of the XVII Convegno Italiano di Ornitologia, Trento, 11–15 September 2013, pp. 43–47.
- Fairhurst, G.D., Treen, G.D., Clark, R.G. & Bortolotti, G.R. 2012. Nestling corticosterone response to microclimate in an altricial bird. *Can. J. Zool.* **90**: 1422–1430.

- Fargallo, J.A., Blanco, G., Potti, J. & Viñuela, J. 2001.** Nestbox provisioning in a rural population of Eurasian Kestrels: breeding performance, nest predation and parasitism. *Bird Study* **48**: 236–244.
- Gal, A. 2006.** Environmental effects on parental care decisions in the Lesser Kestrel (*Falco naumanni*). PhD Thesis, The Hebrew University of Jerusalem (in Hebrew, with English abstract).
- Harris, C.M., Madliger, C.L. & Love, O.P. 2017.** An evaluation of feather corticosterone as a biomarker of fitness and an ecologically relevant stressor during breeding in the wild. *Oecologia* **183**: 987–996.
- Iñigo, A. & Barov, B. 2011.** Species Action Plan for the lesser kestrel *Falco naumanni* in the European Union. SEO/BirdLife & BirdLife International for the European Commission.
- IUCN. 2018.** The IUCN red list of threatened species. DOI: [10.2305/IUCN.UK.2016-3.RLTS.T22696357A87325202.en](https://doi.org/10.2305/IUCN.UK.2016-3.RLTS.T22696357A87325202.en).
- Janes, S.W. 1985.** Habitat selection in raptorial birds. In Cody, M.L. (ed) *Habitat Selection in Birds*, 159–187. Academic Press, New York.
- Kopij, G. & Liven-Schulman, I. 2012.** Diet of the Lesser Kestrel, *Falco naumanni*, in Israel. *Zool. Middle East* **55**: 27–34. DOI: [10.1080/09397140.2012.10648914](https://doi.org/10.1080/09397140.2012.10648914).
- Liven-Schulman, I., Leshem, Y., Alon, D. & Yom-Tov, Y. 2004.** Causes of population declines of the Lesser Kestrel *Falco naumanni* in Israel. *Ibis* **146**: 145–152.
- McClaren, E.L., Kennedy, P.L. & Dewey, S.R. 2002.** Do some Northern Goshawk nest areas consistently fledge more young than others? *Condor* **104**: 343–352.
- Negro, J.J. & Hiraldo, F. 1993.** Nest-site selection and breeding success in the lesser kestrel *Falco naumanni*. *Bird Study* **40**: 115–119.
- Newton, I. 1979.** *Population Ecology of Raptors*. T. and A.D. Poyser, Berkhamsted.
- Perlman, Y. 2013.** The Lesser Kestrel population in Israel – a summary of the 2013 monitoring season. The Society for the Protection of Nature in Israel (in Hebrew). <http://www.tene-eco.co.il/AllSites/230/Assets/333.pdf>.
- Pomarol, M. 1996.** Artificial nest structure design and management implications for the lesser kestrel (*Falco naumanni*). *J. Raptor Res.* **30**: 169–172.
- Raphael, M.G. 1985.** Orientation of American Kestrel nest cavities and nest trees. *Condor* **87**: 437–438.
- Rohrbaugh, R.W. & Yahner, R.H. 1997.** Effects of macrohabitat and microhabitat on nest-box use and nesting success of American Kestrels. *Wilson Bull.* **109**: 410–423.
- Rosenthal, R. 1978.** Combining results of independent studies. *Psychol. Bull.* **85**: 185–193.
- Sarà, M., Campobello, D. & Zanca, L. 2012.** Effects of nest and colony features on Lesser Kestrel (*Falco naumanni*) reproductive success. *Avian Biol. Res.* **5**: 209–217.
- Serrano, D. & Tella, J.L. 2007.** The role of despotism and heritability in determining settlement patterns in the colonial lesser kestrel. *Am. Nat.* **169**: E53–E67.
- Valkama, J. & Korpimäki, E. 1999.** Nestbox characteristics, habitat quality and reproductive success of Eurasian Kestrels. *Bird Study* **46**: 81–88.