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EFFECT OF NEST-SITE MICROCLIMATIC CONDITIONS ON NESTING SUCCESS IN THE LESSER KESTREL (FALCO NAUMANNI)

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in the Lesser Kestrel (*Falco naumanni*)

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Nest-site Selection, Nesting Boxes.

ABSTRACT

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

Aim: (1) 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. (2) To compare microclimatic conditions in the nest, breeding success and order of occupation between nests under tile roofs and artificial nest boxes.

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

Results: (1) Full microclimatic data from 35 nests suggest that percentage of time of extremely low humidity is the major predictor of nest productivity. (2) The urban colony had the lowest breeding success of the three colonies. (3) Sites of more successful nests were occupied earlier. (4) No significant difference in mean productivity between nests in roofs and nest boxes, but nests in roofs were occupied earlier.

Conclusion: Nest microclimate affects nesting success in addition to colony location.

Habitat selection in birds of prey is influenced by climatic conditions, the availability of appropriate prey, the presence of competitors and (in some species) the presence of 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 choice made by the birds themselves (McClaren *et al.* 2002). Cliff and cavity nesters (such as most *Falco* 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 – e.g. the Peregrine Falcon (*Falco peregrinus*), the American Kestrel (*Falco sparverius*), the Eurasian Kestrel (*Falco tinnunculus*) or 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 and 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 from the Iberian Peninsula to Turkey, Azerbaijan, India, Myanmar, and southern China. 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 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 are used in order to augment the declining population, 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, Raphael (1985) reports that orientation influences nest preference by American Kestrels, probably due to thermoregulation advantages. Studying the use of artificial nest boxes by this species also show a preference to particular orientations (Rohrbaugh & Yahner 1997, Butler *et al.* 2009). Examining nest boxes of Eurasian Kestrel in Finland, having different size and orientation, Valkama and Korpimäki (1999) found a preference to certain orientations and to intermediate nest size. Comparing the use of natural nests vs. 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.

Negro and Hiraldo (1993) studied nest site occupancy and success by Lesser Kestrels in three colonies located in churches in southern Spain. 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 Lesser Kestrel to higher nests was found in Sicily (Sarà *et al.* 2012). Comparing artificial and natural nests of Lesser Kestrel in Italy, Bux *et al.* (2008) showed a similar breeding success in nest boxes as in attic nests, but smaller than in natural cavities. Nest boxes installed in Portugal helped in increasing the Lesser Kestrel population (Catry *et al.* 2007). Moreover, the kestrels actually preferred the artificial to the natural nest sites. A study of Lesser Kestrel population in Sicily by Di Maggio *et al.* (2013) demonstrated that nest type (holes vs. nests under roof tiles) and orientation affect 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 fledgling 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*) affects kestrels activity.

In the present work we tried to learn if factors other food limitation, such as microclimate within the Lesser Kestrel nests, have an effect on the nesting success in Israeli colonies.

Methods

The Lesser Kestrel in Israel

The Lesser Kestrel is a summer visitor in 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 usually on cliffs. Clutch size is between 3 to 6 eggs (Cramp & Simmons 1980). The estimated breeding population in Israel is 364 pairs – 63% in rural settlements, 5% in urban and 32% in the open country, mostly in quarries (Perlman 2013). They feed almost exclusively on arthropods, mainly of the 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, 100m asl), representing a rural colony. (2) In the city of Jerusalem (31°47'N 35°13'E, 800m asl), representing an urban colony. (3) On a cliff in the Revaya quarry, on the lower slopes of Mt. Gilboa (32°27'N 35°27'E, 120m asl), 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 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 ca. 30 nests in the colony). In Jerusalem, 5 in 2002 and 5 in 2003 (out of ca. 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 the each nest on the colony cliff.

Statistical Analysis

t-tests and ANOVA were performed wherever appropriate, while the a-parametric Kruskal-Wallis ANOVA, Mann-Whitney U-test and the Spearman's rank correlation analysis were performed in other cases. 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 given for two-tailed alternatives.

For analysing the effect of microclimatic conditions in the nest on nest productivity, six variables were considered as predictors of nest productivity (*NP*) in a generalized linear (GL) model. Five of the variables are microclimatic variables, each measuring a possible microclimatic stress: The minimal temperature recorded in the nest throughout the nesting period (*MinTemp*), the maximal 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 5 and the 95 percentiles of the humidity distribution in the nests). The sixth predictor (*Colony*) is a string variable. Alternative

models were compared using the corrected Akaike's Information Criterion (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. They enabled us to determine the occupation order of the nests in each colony unequivocally, and thus to correlate the occupation order with productivity and other nest features.

Results

Productivity

Mean productivity per nest (i.e., the mean number of nestlings fledged per pair) are given (\pm se) for each of the six Year \times Colony combinations (Table 1). There were no significant differences among colonies (Kruskal-Wallis test, $P = 0.360$) and no significant differences among years (one-way ANOVA, $F_{2,36} = 0.382$, $P = 0.685$).

Considering only successful nests, there were still no significant differences among years (one-way ANOVA, $F_{2,21} = 0.599$, $P = 0.559$), but there were significant differences among colonies (one-way ANOVA, $F_{2,21} = 5.353$, $P = 0.013$). Tukey's post-hoc analysis indicates significant differences both between Jerusalem and Alona ($P = 0.045$) and between Jerusalem and Gilboa ($P = 0.013$), with Jerusalem achieving the lower productivity in both comparisons (Table 1, shaded column).

Effect of microclimatic conditions in the nest on nest productivity

For this analysis, we had complete data on 35 nests. The five micro-climatic variables plus *Colony* were considered as predictors of nest productivity (*NP*), hence we have 64 possible combinations of predictors in the GL analysis. Using the Akaike

information criterion, we first compared between the six simple, single-predictor GL models (Table 2), to check if there are any predictor that carry very little weight and therefore can be dropped. The one with the least loss of information was, by far, the model with *LowHum* as a predictor of nest productivity (having an Akaike weight of 89.5%), with the models *MaxTemp* and *HighHum* lagging much behind (weights of 3.7% and 3.3%, respectively). *Colony* achieved 1.5%, while *MinTemp* and *Temp* \geq 40° achieved negligible weights of 1.1% and 0.9% only. Thus, for the second round, we compared all 16 possible models having any subset of *LowHum*, *MaxTemp*, *HighHum* and *Colony* as predictors of *NP* (Table 3). Again, the model with *LowHum* as a sole predictor of nest productivity was the best, better by 112% than the model with *LowHum* and *MaxTemp* as predictors, by 117% than the model with *LowHum* and *HighHum* as predictors, and by 136% than the model with *MaxTemp* and *Colony* as predictors. Still, adhering to the suggested practice of considering all models having $\Delta\text{AICc} \leq 2$ (e.g., Burnham *et al.* 2011), we will not discard the three latter models. The relatively high score of the model with *MaxTemp* and *Colony* as predictors is not very surprising in light of the fact that *Colony* proves to be a strong predictor of *LowHum* in a GL model: The omnibus test that compares the fitted GL model against the intercept-only model has $\chi^2_2 = 27.117$ ($P < 0.001$).

For model averaging, we considered only the three numeric variables (*LowHum*, *MaxTemp* and *HighHum*) as predictors of *NP* in a standardized linear regression model. The average standardized linear model, produced by a weighted average of the eight relevant models of Table 3 (each weighed by its Akaike weight), is: $NP = 1.831 - 0.430 \times LowHum - 0.053 \times MaxTemp + 0.050 \times HighHum$. 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 *NP*, *LowHumid* 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 a mere 0.017. F statistics and P values for each of these three 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 merely $R^2 = 0.083$ ($F_{1,33} = 2.994$, $P = 0.093$), and the decrease in productivity is only 0.095 chicks per 1°C increase in mean maximal temperature in the nest.

Considering only successful nests in the GL model analysis, and focusing only on *LowHumid* and *MaxTemp* as predictors, we see that while *LowHumid* retains its central role as a predictor of *NP*, the importance of *MaxTemp* is somewhat increased (Table 4).

Productivity and occupation order

In each of the six Colony \times 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. We found a negative correlation between nest productivity and its rank in the order of occupation (Table 5). 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 days relative humidity in the nest was below 17% (*LowHum*) and order of occupation (Table 6). The combined significance level was $P = 0.006$, indicating that nests having smaller percentage of low humidity were occupied earlier.

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 maximum temperature were not 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: $P = 0.114$; 2003: $P = 0.048$; 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 Liven-Schulman *et al.* (2004) study, who studied 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 to nest productivity. Microclimatic conditions evidently have an impact on the growth and survival of altricial nestlings. Studying corticosterone level in feathers of Tree Swallow (*Tachycineta bicolor*) nestlings, Fairhurst *et al.* (2012) have demonstrated corticosterone is positively correlated with increased temperature variability in the nest and maximum, but not minimum, nest temperature. Our study of microclimate conditions (temperature and humidity) in 35 Lesser Kestrel nests in Israel indicates that the main factor influencing the productivity of a nest, measured by the number of fledglings, is 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. Our study, which incorporated both the effects of temperature and humidity, indicates that dehydration is probably the main factor for nestling mortality. 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.

More successful nests, i.e., nests that fledged a larger number of young, were seized earlier by the nesting parents. A possible explanation could be that earlier occupation of nests is by stronger and more experienced parents, which naturally produce more fledglings. Nevertheless, the correlation found between the most

significant microclimatic variable, namely the percentage of days during which humidity in a nest is below the threshold, and the order of nest occupation, suggests that the nesting parents can probably perceive a-priori the quality of the various nest sites.

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 could be measured) 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 (Catry *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 slowed chicks' growth rate and increased chick mortality (Catry *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.

Turning aside from the microclimatic explanations, we want to mention the paper by Fargallo *et al.* (2001). They found that Eurasian Kestrel chicks from nest boxes showed a higher intensity of infection by the ectoparasite *Carnus hemapterus* than chicks from natural nests.

Although microclimatic conditions in the nest affect nesting success, there are other, not less important factors, such as nest height from the ground, colony location and human disturbance. The low nesting success in Jerusalem is 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.

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References

- 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. *Conservation 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(3): e0174090. doi: 10.1371/journal.pone.0174090
- Catry, 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. *Conservation Evidence* **4**: 54–57.
- Catry, 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, U.K.
- 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. In 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. & Bortolotta, 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).
- 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
- Janes, S.W.** 1985. Habitat selection in raptorial birds. In: Cody, M.L. (ed.) *Habitat Selection in Birds*, pp 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
- 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, U.K.

- 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.
- Valkama, J. & Korpimäki, E.** 1999. Nestbox characteristics, habitat quality and reproductive success of Eurasian Kestrels. *Bird Study* **46**: 81–88.

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

Table 2. Akaike Information Criterion (AICc) for six single-predictor GL models.

The dependent variable is nest productivity (*NP*).

Predictor	AICc	Δ AICc	Akaike Weight
<i>LowHum</i>	134.759	0	0.895
<i>MaxTemp</i>	141.139	6.380	0.037
<i>HighHum</i>	141.350	6.591	0.033
<i>Colony</i>	142.877	8.118	0.015
<i>MinTemp</i>	143.478	8.719	0.011
<i>Temp</i> \geq 40°	144.060	9.301	0.009

Table 3. Akaike Information Criterion (AICc) for 16 GL models. The dependent variable is nest productivity (*NP*).

<i>Max Temp</i>	<i>Low Hum</i>	<i>High Hum</i>	<i>Colony</i>	AICc	Δ AICc	Akaike Weight	Evidence Ratio
	✓			134.759	0	0.302	
✓	✓			136.262	1.503	0.142	2.120
	✓	✓		136.305	1.546	0.139	2.166
✓			✓	136.474	1.715	0.128	2.357
✓	✓		✓	137.066	2.307	0.095	3.169
✓	✓	✓		138.174	3.415	0.055	5.515
✓		✓	✓	139.107	4.348	0.034	8.793
	✓		✓	139.883	5.124	0.023	12.962
✓	✓	✓	✓	139.988	5.229	0.022	13.660
✓				141.139	6.380	0.012	24.288
		✓		141.350	6.591	0.011	26.991
✓		✓		141.647	6.888	0.010	31.312
	✓	✓	✓	141.771	7.012	0.009	33.315
Intercept-only model				141.779	7.020	0.009	33.448
			✓	142.877	8.118	0.005	57.916
		✓	✓	143.886	9.127	0.003	95.919

Table 4. Akaike Information Criterion (AICc) for four GL models, involving only successful nests (i.e., nest having positive productivity). The dependent variable is nest productivity (*NP*).

Predictors	AICc	Δ AICc	Akaike Weight
<i>LowHum & MaxTemp</i>	74.551	0	0.510
<i>LowHum</i>	75.182	0.631	0.372
<i>MaxTemp</i>	78.371	3.820	0.075
Intercept Only	79.499	4.948	0.043

Table 5. Spearman's rank correlation coefficient between nest fledgling numbers and the order by which nests were occupied.

Colony	Year	Number of nests	Spearman's ρ	<i>P</i> 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

Table 6. Spearman's rank correlation coefficient 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	<i>P</i> 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