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Source: Journal of Raptor Research, 41(2) : 143-149

Published By: Raptor Research Foundation

URL: https://doi.org/10.3356/0892-1016(2007)41[143:TEODNT]2.0.CO;2

J. Raptor Res. 41(2):143–149

THE EFFECT OF DIFFERENT NEST TYPES ON THE BREEDING SUCCESS OF EURASIAN KESTRELS (*FALCO TINNUNCULUS*) IN A RURAL ECOSYSTEM

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KEY WORDS: *Eurasian Kestrel*; Falco tinnunculus; *breeding success*; *nest box*; *nest type*; *weather.*

Breeding success of birds can be affected by different factors such as food availability (Cavé 1968, Village 1982, Wiehn and Korpimäki 1997), competition (Nilsson 1984, Korpimäki 1987, Hakkarainen and Korpimäki 1996), predation (Newton 1979, Sergio et al. 2003), risk of predation (Skutch 1949, Snow 1962, 1978, Slagsvold 1982), territoriality (Village 1983), human disturbance (Gutzwiller et al. 2002), laying date (Daan et al. 1988, Korpimäki and Wiehn 1998, Aparicio 1994), and abiotic factors such as temperature and rainfall (Kostrzewa and Kostrzewa 1991, Avilés et al. 2000, Salvati 2002).

The Eurasian Kestrel (*Falco tinnunculus*; hereafter ''kestrel''), is a small open-country raptor that (like most falcons) does not build its own nest but, unlike most raptors, breeds in both open-type nests (e.g., cliff ledges, corvid nests) and closed-type nests (e.g., cavities; Village 1990). In previous studies, breeding success of kestrels nesting in cavities and nest boxes was higher (Kostrzewa and Kostrzewa 1997), and such nest types were more favored (Korpimäki 1983), compared to open-type stick nests of other species (Village 1998, Valkama and Korpmäki 1999), possibly because of decreased risk of predation. Reproductive rates of kestrels in other studies are only rarely reported

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for the different nest types separately (as in Kostrzewa and Kostrzewa 1997, Valkama and Korpmäki 1999, Fargallo et al. 2001), but commonly grouped together (Pikula et al. 1984, Gil-Delgado et al. 1995, Van Zyl 1997). Consequently, there is a need to verify whether differences in reproductive rates may also be due to the different nest types, in order to allow comparison within and between studies.

Three kestrel nest types were used in this study: two different types of nest boxes (i.e., artificial cavities), the larger of which also represents a limiting resource for the larger Barn Owls (*Tyto alba*) in the study area, and natural open-type nests in date palms (*Phoenix dactylifera*). By studying three different nest types, each influenced by different factors and all used by kestrels within the same region, we were able to compare how nest type can influence kestrel breeding success. Additionally, although the biology of kestrels is well known in Europe (Village 1990), it has not been studied in detail in the Middle East. We also investigated the effects of temperature, rain, and diet on reproductive rate, to further our understanding of how different factors affect breeding success.

METHODS

Study Areas. The study site consisted of agricultural fields, orchards, and plantations in Kibbutz Sde Eliyahu, located in the Jordan Rift Valley, Israel (32°30′N, 35°30′E), 7 km southwest of the city of Beit Shean and 150–250 m below sea level. The climate is arid with maximum and minimum mean daily temperatures (during March and July 1999) of 32.3°C and 16.7°C, respectively, and average yearly rainfall of 267 mm (for 2001–2006; M. Hyman pers. comm.).

The majority of the study site (combined area of 989 acres) is used for organic agriculture, primarily crop fields and date plantations. The crop fields include fodder (wheat, sweet corn, alfalfa, clover, vetch and oats), grain crops and seeds (wheat and sweet corn) and spices and herbs (oregano, hyssop, basil, and dill). The date palm plantation has ten different varieties, the oldest planted in the early 1950s.

Nest Types. Kestrels in the study site breed in three different nest types, two of which are human-made (small and large nest boxes), and one natural (date palms). Sixty large nest boxes (50 cm wide × 75 cm long × 50 cm high; entrance hole 25 cm high × 15 cm, mounted 2.5–3 m aboveground) were placed in the fields and date palm plantations from 1993–1997 with the intention that Barn Owls would use them (Aviel et al. 2003). Although these nests were the lowest in height of the three nest types in this study, kestrels have been shown to nest successfully at similar heights in Europe (Cavé 1968) and in other locations in Israel (M. Charter unpubl. data.). In addition, unlike Europe (Village 1990, Valkama and Korpmäki 1999), our study site does not contain arboreal mammals; thus, clutch and brood predation by mammals is not a factor. Eleven small nest boxes were specifically built for kestrels in 1998 (50 cm wide × 30 cm long × 30 cm high; entrance hole 22 cm high × 15 cm, attached to date palms at 5–6 m). Because of the small size of these boxes, Barn Owls do not use them as nest sites but do occasionally use them as roosts. The third type of nests, natural nests on date palms, are open sites in which kestrels nest in the offshoots (clipped palm branches). The number of potential nest sites in the date plantations is estimated at up to 13 nests per year and changes from year to year are mainly due to the partial destruction of nests by the kestrels during the breeding season and the effects of weather during the winter.

Breeding Success. Active nests in the date palms were located by direct observation of the kestrels' breeding behavior, mainly copulating close to the nests (Village 1990). From 1999–2006, for each breeding attempt (defined as a nest in which eggs were laid; Steenhof 1987), we recorded the date of egg-laying, hatching, and fledging of young when possible, along with clutch size, brood size (number of young observed in nest during first visit, <1 wk after hatching) and the number of young fledged (23–27 d old). When laying date was unknown, it was determined by backcalculating using an incubation period of 28 d (Cramp 1985). During years when nests were visited late, only breeding parameters that were known were included in the analysis. We calculated the following: (a) hatching success as the percentage of eggs that hatched within each clutch; (b) the percentage of young that fledged from each brood for all pairs that hatched at least one egg. (c) egg productivity as the percentage of eggs per nest that hatched and fledged young (d) brood size per breeding attempt (e) the number of young fledged per breeding attempt; and (f) the number of young per successful nest, where a successful nest was defined as one that produced at least one chick that fledged. Breeding data were recorded for each breeding attempt unless stated otherwise.

Weather Data. A permanent weather station located at Kibbutz Sde Eliyahu provided data on precipitation and daily temperatures (mean, minimum and maximum) from 2001–2006. Weather data were divided into two periods: Winter (1 November–28 February) and breeding season (1 March–31 July). The daily mean temperatures, maximum temperatures, minimum temperatures, and humidity for the winter and breeding season were calculated by averaging daily values. Rainfall was recorded as the total amount of rainfall for each period. Weather data for winter and breeding season were tested for correlations with annual kestrel clutch size, number of young fledged, and percentage hatching success of the three nest types combined and separately (160 Spearman rank correlations; $N = 6$ yr for all correlations). Only significant ($P < 0.05$) correlations are presented.

Pellet Collection and Analysis. Kestrel pellets were collected weekly from nests (female and nestlings) and roosts (adults) during the breeding season. Pellets were dried and placed in individually numbered bags. Unlike most owl pellets, which are usually soaked in water or other liquid prior to dissection, the kestrel pellets were taken apart dry, because soaking them makes identification of invertebrate remains in the matrix difficult (Village 1990). Using tweezers and a dissecting microscope, pellets were pulled apart and prey items separated. The results are presented as percentage frequency of occurrence: the proportion of the total number of pellets containing a given prey item.

Mammals were identified by their teeth and femur, birds by feathers, and reptiles by teeth and scales. All invertebrates were classified as a single group. Unknown prey items were identified by comparison with the collection of the National Museum of Natural History at Tel Aviv University.

Data Analyses. Data are presented as means ± SE. All tests were two-tailed. To account for nest boxes used in multiple years of the study (probably by the same pairs), we included a random variable for year in each test. The effects of year and nest type for all breeding parameters (clutch size, brood size, number of young fledged per breeding attempt, hatching success, percentage of young fledged, percentage egg productivity, and laying date) were analyzed using a 2-way ANOVA and Bonferroni correction for multiple comparisons. All percentages were arcsin square-root transformed prior to analyses.

Spearman correlations were used to analyze correlations and Pearson chi-square were used for comparing nest success between locations. For nests used in more than one breeding season, we randomly selected one year of data when Spearman correlations were used. Statistical analyses were performed using Statistica 7.1 software.

RESULTS

Breeding Success. From 1999–2006, we monitored 137 kestrel breeding attempts in 95 different nests. The number of laying pairs per year varied from 13 to 24 and individual nests were used 1 to 5 times during the study. Of the 137 breeding attempts, 44 were in large nest boxes, 37 in small nest boxes, and 56 in date palms. Laying dates across all nest types were negatively correlated with clutch size (Spearman correlation = −0.47, N = 33, $P < 0.01$) and number of young fledged (Spearman correlation = −0.40, N = 43, $P < 0.01$). Clutch size and laying dates were negatively correlated in the small nest boxes (Spearman correlation = −0.65, N = 12, $P < 0.05$) and large nest boxes (Spearman correlation = −0.88, N = 6, $P < 0.05$) but not in the date palms (Spearman correlation = −0.15, N = 15, $P < 0.18$). Number of young fledged and laying dates were negatively correlated in the small nest boxes (Spearman correlation = −0.59, N = 12, $P < 0.05$) but not in the large nest boxes (Spearman correlation = −0.57, N = 11, $P < 0.10$) and date palms (Spearman correlation = −0.39, N = 20, $P < 0.10$). No differences were found in laying dates between nest types (Table 1).

Mean clutch size per breeding attempt across all nest types was 4.45 ± 0.10 (N = 82) and there was a difference among the three nest types (Table 1). Clutch size of kestrels nesting in the small nest boxes was greater than that of pairs in the date palms (Table 1). Mean brood size per breeding attempt across all nest types was 2.56 ± 0.19 (N = 115) and there was a significant difference among the three nest types; brood size of kestrel laying pairs nesting in the large nest boxes was lower than that of kestrels breeding in the small nest boxes and date palms (Table 1). Mean number of young fledged per breeding attempt across all nest types was 2.29 ± 0.16 (N = 137), with more young fledged per attempt in small nest boxes than in large (Table 1). The number of young fledged per successful nest among the three nest types also differed (Table 1),

Table 1. Comparison of breeding parameters (mean ± 1 SE and sample size for clutch size, brood size, number of young fledged per breeding attempt, number of young fledged per successful nest, hatching success, percentage of young fledged, egg productivity, and laying date) among kestrel pairs breeding in different nest types (date palms, small and large nest boxes) and years at Kibbutz Sde Eliyahu, Israel, using a 2-way ANOVA. In all tests the effect of year and effect of interaction (nest type × year) were not significant ($P > 0.05$). Different letters indicate significant difference between nest types (Bonferroni multiple comparisons, $P < 0.05$; i.e., when no differences were found between two nest types, they have the same letter). When a nest type has both letters (i.e., ab), no significant differences were observed between it and the other two nest types (a and b).

MEASURE OF REPRODUCTIVE RATE	SMALL NEST BOXES	LARGE NEST BOXES	DATE PALMS	F	P
Clutch size	4.90 ± 0.18 (31)^{a}	4.37 ± 0.11 (19)^{ab}	4.06 ± 0.15 (32)^{b}	3.31	0.04
Brood size	3.36 ± 0.38 (33)^{a}	1.64 ± 0.32 (36)^{b}	2.70 ± 0.23 (46)^{a}	4.34	0.02
Number of young fledged/breeding attempt	3.03 ± 0.34 (37)^{a}	1.88 ± 0.30 (44)^{b}	2.13 ± 0.19 (56)^{ab}	3.24	0.04
Number of young fledged/successful nest	3.86 ± 1.46 (29)^{a}	3.61 ± 0.22 (23)^{a}	2.70 ± 0.16 (44)^{b}	8.11	0.001
Percentage hatching success	65.1 ± 7.2% (32)^{a}	26.0 ± 7.5% (30)^{b}	56.8 ± 5.9% (34)^{a}	3.29	0.04
Percentage of young fledged	89.9 ± 4.1% (26)^{ab}	98.8 ± 1.3% (16)^{a}	74.2% ± 5.5% (39)^{b}	4.61	0.01
Percentage egg productivity	59.5 ± 6.9% (31)^{a}	26.2 ± 7.6% (29)^{b}	37.9% ± 5.6% (34)^{ab}	2.71	0.07
Laying date	7 April ± 4.1 (12)^{a}	2 April ± 5.8 (11)^{a}	6 April ± 3.2 (20)^{a}	1.84	0.17

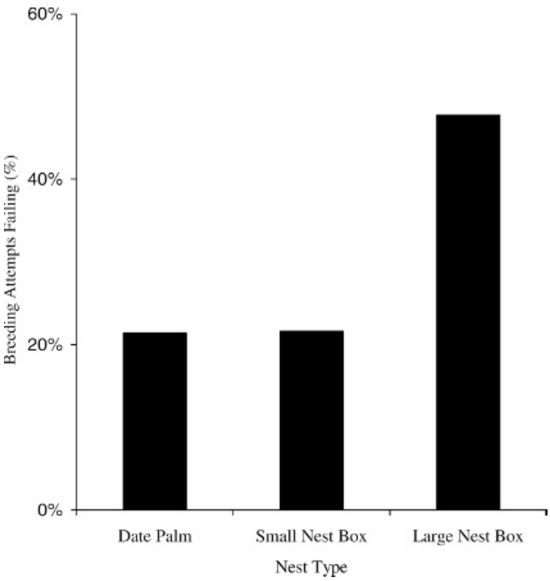

Figure 1. Percentage of Eurasian Kestrel breeding attempts (nests in which eggs were laid) failing to produce young, as a function of nest type, at Kibbutz Sde Eliyahu, Israel, 2002–2004. Distribution differed significantly (Pearson $\chi^2 = 9.79$, $P < 0.01$).

with the number fledged in date plantations lower than that in both the small and large nest boxes (Table 1).

Mean hatching success for all nest types was 50.0% ± 4.3% ($N = 96$), but kestrels nesting in large nest boxes had lower hatching success than pairs using small nest boxes and date palms (Table 1). Mean percentage of nestlings fledged for all pairs that hatched at least one egg was 84.1% ± 3.0% ($N = 81$) for all nest types, and the percentage of young fledged from large nest boxes was higher than that from date palms but similar to that from small nest boxes (Table 1). Mean percentage egg productivity for all nest types was 41.4% ± 4.06% ($N = 94$), and egg productivity of kestrels breeding in small nest boxes was higher than that of those in large nest boxes but not those in date palms (Table 1).

Nest Failure. During 1999–2006, 41 of 137 breeding attempts failed to produce young, with 85% failing during the egg stage ($N = 35$) and the remainder during the nestling stage ($N = 6$). More birds nesting in the large breeding boxes failed to fledge young than those nesting in the small nest boxes and in the date palms (Fig. 1). In the large nest boxes ($N = 17$ failures), 71% of clutches were abandoned, 19% failed due to known Barn Owl interference, and 10% of clutches did not hatch. Twenty-two of 96 breeding attempts that were successful in producing at least one fledged young failed partially (at least one young died in the nest), of which fewer kestrel pairs breeding in the large nest boxes ($N = 1$) failed partially than in the small nest boxes ($N = 7$; Fisher Exact Test $P < 0.05$) and date palms ($N = 14$; Fisher Exact Test $P < 0.01$).

Weather. During the winter, only the combined clutch size of all three nest types was correlated with the amount of rainfall (Spearman correlation = -0.81, $P < 0.05$). During the breeding season, the percentage hatching success of the combined nest types was negatively correlated with the minimum (Spearman correlation = -0.83, $P < 0.05$) and mean temperatures (Spearman correlation = -0.83, $P < 0.05$). Only in pairs breeding in date palms was percentage hatching success negatively correlated with maximum temperatures (Spearman correlation = -0.89, $P < 0.05$) and number of young fledged negatively correlated with mean temperatures (Spearman correlation = -0.94, $P < 0.01$); while percentage hatching success was positively correlated with humidity (Spearman correlation = 0.94, $P < 0.01$). The number of young fledged and percentage hatching success were negatively correlated with amount of rainfall during the breeding season (Spearman correlation = -0.89, $P < 0.05$ and Spearman correlation = -0.94, $P < 0.001$, respectively) only in pairs breeding in the large nest boxes.

Diet. During the 2002 breeding season, 147 pellets were collected from five large boxes, 185 pellets from five small nest boxes, and 217 pellets from 11 date palm nests. No significant difference was observed in the occurrence of remains of small mammals, reptiles, birds, and invertebrates found in pellets from kestrel pairs breeding in the three nest types (Table 2). During this same year, 189 pellets were collected from eight roosts of adult kestrels: 47% of the pellets had remains of small mammals, 51% birds, 23% reptiles and 75% invertebrates. After combining the above data from the 21 nests and comparing them with the data of the roosts, we found that the frequency of occurrence of small mammals was higher in the pellets collected from the nests than in those from roosts ($t_{27} = 3.59$, $P < 0.01$), whereas no difference was found in the occurrence of reptiles ($t_{27} = 0.07$, $P = 0.94$), birds ($t_{27} = 1.32$, $P = 0.20$), or invertebrates ($t_{27} = -1.09$, $P = 0.28$).

DISCUSSION

In this study, we examined the reproductive rates of kestrels breeding in three types of nest boxes. Kestrels nesting in the large nest boxes had (1) the lowest brood size and percentage of eggs hatching, (2) a lower number of fledged young and percentage of egg productivity than in the smaller nest boxes, and (3) more breeding failure than in the other two nest types. In other studies, earlier-breeding pairs generally lay larger clutches (Cavé 1968, Dijkstra et al. 1982, Village 1990, Aparicio 1994) and have higher reproductive rates. However, because we did not find differences in laying dates among nest types, we do not believe that the failures of pairs in the large nest boxes were the result of poor quality of birds or territories, as reflected by the date of egg-laying. In addition, when the breeding attempts that failed were excluded, kestrels in the large nest boxes demonstrated less partial failure (at

Table 2. Comparison of prey occurrence in kestrel pellets[1] collected from kestrel pairs breeding in large nest boxes ($N = 5$), in small nest boxes ($N = 5$), and in date palms ($N = 11$) during the 2002 breeding season at Kibbutz Sde Eliyahu, Israel.

PREY TYPE	PERCENTAGE FREQUENCY OF OCCURRENCE			PARAMETRIC ANOVA STATISTICS P
	SMALL NEST BOXES	LARGE NEST BOXES	DATE PALM TREES	
Small mammals	79%	86%	78%	$F_{2,18} = 0.28$, $P = 0.76$
Birds	52%	36%	56%	$F_{2,18} = 1.12$, $P = 0.35$
Reptiles	31%	31%	41%	$F_{2,18} = 0.41$, $P = 0.67$
Invertebrates	59%	52%	69%	$F_{2,18} = 0.61$, $P = 0.55$

[1] Number of pellets: large nest box = 147, small nest box = 185, date palms = 217.

least one nestling died in the nest) than birds in the other two nest types.

Breeding success of some kestrel populations is correlated with both temperature and rain (Cavé 1968, Newton 1979, Kostrzewa and Kostrzewa 1991, Kostrzewa and Kostrzewa 1994), whereas other populations seem unaffected (Salvati 2002). However, none of the above studies compared the effects of weather among different nest types. The only weather variable of the winter season that may have affected breeding success in the spring was the amount of rain, which was negatively correlated with hatching success when all nest sites were combined. Even though only 16% of the annual rainfall occurred during the breeding season, the number of fledged young per breeding attempt and the hatching success of the birds nesting in the large nest boxes decreased with increasing rain. Unlike kestrels breeding in Europe, which are affected by winter temperatures and snow cover (Kostrzewa and Kostrzewa 1991), those breeding in Israel experience mild winters without snow, but higher temperatures during the breeding season, which was negatively correlated with hatching success. In the dry, hot, Mediterranean climate, heat rather than cold may pose difficulties for breeding birds. In Israel, heat exhaustion and mortality have been found in entire broods of both Barn Owls (K. Merom unpubl. data.) and Lesser Kestrels (*Falco naumanni*; Bobek et al. 2003) in nest boxes after a heat wave. Hatching success and the number of young fledged per breeding attempt were negatively correlated with temperature in this study. In comparison, breeding parameters of kestrels nesting in a northern Mediterranean region (Salvati 2002) were not affected by temperature. Interestingly, hatching success in kestrels nesting in date palms increased with humidity, something not reported in other studies.

Insufficient food resources has been the main cause assigned to nest failures in previous kestrel studies (Village 1990). In the present study, however, we have no knowledge of the food availability or food delivery rate to the young. Nevertheless, we concluded that diet differences probably were not responsible for differences in production among the three nest types, as pellets from kestrels in the three nest types contained similar frequencies of prey types.

As the kestrels in our single study site inhabited overlapping home ranges, human disturbance was expected to similarly affect breeding success in the different nest types. In addition to kestrels, Barn Owls also nest in the large nest boxes. These Barn Owls not only initiate breeding earlier, but also are physically larger and are known to occasionally usurp nest sites occupied by kestrels (Bunn et al. 1982, Roulin 2002). It is possible that the high percentage of nest failure, low hatching rate, and low percentage egg productivity of pairs breeding in the large nesting boxes were mainly due to competition with Barn Owls over the nest sites.

The percentage of nests failing to fledge young in the large nest boxes (48%; all loss occurring during the egg stage) was the greater than that in nine studies of rural kestrels in Europe (3–42%, 24% average; Pikula et al. 1984, Bonin and Strenna 1986, Village 1986, Village 1990, Plesník and Dusík 1994, Kostrzewa and Kostrzewa 1997, Village 1998, Avilés et al. 2000). In other studies, kestrels typically preferred nest boxes over natural open nests (Korpimäki 1983, Village 1990) and it was therefore surprising to find such a high percentage of failure in pairs breeding in large nest boxes in Israel. Although Barn Owls were clearly responsible for only 19% of failures in the large nest boxes, we suspect that Barn Owls might have been responsible for several other abandoned kestrel clutches. We were unable to determine the cause of abandonment for kestrel clutches when Barn Owls were not present.

The smaller clutch size and decreased breeding success (number of fledglings per successful nest) of kestrels breeding in the date palms may have been due to risk of predation (Skutch 1949, Snow 1962, 1978). In our study site, Carrion Crows (*Corvus corone*), and Eurasian Jays (*Garrulus glandarius*), are potential nest predators of kestrels. The open-type nests in the date palms are much more difficult to defend from predators than nest boxes, in which the nest entrance can be blocked by an adult kestrel. Additionally, the presence or absence of the female can be detected more easily in the open nest. Birds under threat of such intrusions may benefit from a reduction in clutch size (review by Slagsvold 1982). Other observational studies also found the breeding success of kestrels in open nests to be lower (Kostrzewa and Kostrzewa 1997, Fargallo et al. 2001).

In the present observational study, we found differences in reproductive rates among kestrels breeding in different nest types. Both competition with another raptor species for nest sites and the risk of predation may influence breeding success, but experimental studies are needed to verify and provide a better understanding of these interactions in raptors. Our study also underscores the importance of reporting raptor breeding success by nest types. This is particularly important when comparing results between studies, because the findings may be influenced primarily by the different nest types, rather than by variation between populations.

EL EFECTO DE DIFERENTES TIPOS DE NIDO SOBRE EL ÉXITO REPRODUCTIVO DE *FALCO TINNUNCULUS* EN UN ECOSISTEMA RURAL

RESUMEN.—Estudiamos la tasa reproductiva de *Falco tinnunculus* en diferentes tipos de nido artificiales y naturales en una región rural de Israel. Los nidos se clasificaron en tres tipos: (1) nidos grandes artificiales de tipo cerrado (i.e., cajas de nidificación), (2) nidos pequeños artificiales de tipo cerrado (i.e., cajas de nidificación) o (3) nidos naturales de tipo abierto (i.e., nidos en palmas datileras *Phoenix dactylifera*). El éxito reproductivo fue menor en las cajas de nidificación grandes: el porcentaje de los nidos en que los huevos eclosionaron fue el más bajo, al igual que el tamaño de la parvada, el número de pichones que abandonaron el nido por puesta de la pareja y el porcentaje de productividad de los huevos. Un número significativamente menor de parejas fueron exitosas en las cajas de nidificación grandes en producir al menos un volantón que en los otros dos tipos de nido. Esto posiblemente se debe a competencia por los sitios de nidificación con lechuzas *Tyto alba.* El tamaño de las nidadas fue significativamente menor en los nidos ubicados en palmas que en las cajas de nidificación pequeñas, lo que podría estar relacionado con el riesgo de depredación de los nidos. Durante el invierno, la cantidad de lluvia estuvo correlacionada negativamente con el tamaño de la nidada, mientras que durante la época reproductiva, la temperatura del aire se relacionó negativamente con el éxito de eclosión. A diferencia de lo que sucede en Europa, las aves que nidificaron en el clima mediterráneo se vieron afectadas por las temperaturas altas, y no por las temperaturas bajas. Como los parámetros reproductivos aparentemente difirieron entre los tipos de nido en nuestro estudio, sugerimos que los informes sobre el éxito de nidificación de las aves rapaces deben proveer datos separados para distintos tipos de nido.

[Traducción del equipo editorial]

ACKNOWLEDGMENTS

We are especially grateful to Kibbutz Sde Eliyahu for lodgings and assistance during all stages of the research. Special thanks to Shaul Aviel who assisted in the field and made this research possible, Steve Charter for his assistance in the date palms plantation, Michael Hyman for the weather data from Kibbutz Sde Eliyahu, Anthony Van Zyl for comments on the text, and Naomi Paz for editorial assistance.

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Received 23 October 2006; accepted 13 March 2007
Associate Editor: Vincenzo Penteriani