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BREEDING SUCCESS AND ITS CORRELATION WITH NEST-SITE CHARACTERISTICS: A STUDY OF A GRIFFON VULTURE COLONY IN GAMLA, ISRAEL

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ABSTRACT.—Gamla Nature Reserve once held the largest colony of nesting and roosting Griffon Vultures (*Gyps fulvus*) in Israel, with 45 to 57 pairs nesting at the colony during our study years (1998–2002), and up to 140 individuals roosting on the canyon's cliffs. Nevertheless, the fledging success there was very low: only 34% of breeding attempts (nest with eggs laid) resulted in fledged young during our study. Poisoning and hunting were the main causes of mortality, but in addition, a shortage of appropriate nesting places may also have been an important limiting factor. Fledging percentage was correlated with nest-site use and "attractiveness": nest sites with greater fledging percentage also had more breeding attempts and were inhabited earlier in the nesting season. The main physical characteristic that enhanced breeding success was the type of nest site; nests in caves were more successful and were used for more breeding attempts than nests that were exposed from above. The influence of microclimatic conditions on nesting success was emphasized by the differences in the intensity of parental care, particularly activities associated with thermoregulation, between parents at the different types of nest sites. Parents at exposed nests invested substantially more time in thermoregulation (i.e., brooding or shading the young), an investment that was negatively correlated with breeding success.

KEY WORDS: *Griffon Vulture*; Gyps fulvus; *breeding success*; *nesting success*; *nest-site characteristics*; *parental care*; *thermoregulation*.

ÉXITO REPRODUCTOR Y SU CORRELACIÓN CON LAS CARACTERÍSTICAS DEL LUGAR DE NIDIFICACIÓN: ESTUDIO DE UNA COLONIA DE *GYPS FULVUS* EN GAMLA, ISRAEL.

RESUMEN.—La Reserva Natural de Gamla albergaba la mayor colonia de nidificación y dormidero de *Gyps fulvus* en Israel, con 45 a 57 parejas nidificando en la colonia durante nuestros años de estudio (1998–2002), y hasta 140 individuos posados en los roquedos del cañón. Sin embargo, el éxito de los volantones que dejan el nido fue muy bajo: durante nuestro estudio, sólo el 34% de los intentos de cría (nidos con puestas) produjo un pollo que dejó el nido. Las principales causas de mortalidad fueron el envenenamiento y la caza, aunque también una disminución de los lugares apropiados para el establecimiento de los nidos podría haber sido un factor limitante importante. El éxito de los pollos que dejan el nido estuvo correlacionado con el uso y el "atractivo" del lugar de nidificación: los nidos con mayor éxito de los pollos que dejan el nido también presentaron una mayor cantidad de intentos de cría y fueron ocupados antes en la época reproductora. La principal característica física que permitió el éxito reproductivo fue el tipo de lugar de nidificación; los nidos ubicados dentro de cuevas fueron más exitosos y fueron utilizados en un mayor número de intentos de cría que los nidos que estuvieron expuestos por arriba. La influencia de las condiciones microclimáticas en el éxito de cría estuvo acentuada por las

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diferencias en la intensidad del cuidado parental entre padres en diferentes tipos de lugares de nidificación, particularmente por las actividades asociadas con la termorregulación. Las parejas reproductoras con nidos expuestos invirtieron sustancialmente más tiempo en la termorregulación (i.e., incubando o sombreando a los pollos), una inversión que estuvo correlacionada negativamente con el éxito reproductor.

[Traducción del equipo editorial]

Habitat loss, particularly of appropriate nest sites, is one of the main causes for avian population decline and for the extirpation of a species from an area. Raptors, especially cliff-nesters, are among the groups that are clearly limited by the availability of nesting places (Newton 1979). Almost half of the 16 species of Old World vultures are cliff-nesters, and four of these cliff-nesters (Griffon Vulture [*Gyps fulvus*], Rüppell's Vulture [*G. rueppellii*], Cape Vulture [*G. coprotheres*], and Indian Vulture [*G. indicus*]) are colonial breeders. Studies on their habitat preferences, nest-site selection, and breeding success are numerous (e.g., Brown and Piper 1988, Mundy et al. 1992, Fernández et al. 1998, Iezekiel et al. 2004, López-López et al. 2004, García-Ripollés et al. 2005, Xirouchakis and Mylonas 2005, Gavashelishvili and McGrady 2006, Margalida et al. 2007, Monsarrat et al. 2013, Demerdzhiev et al. 2014). Most of these studies emphasize the importance of proximity to food resources, the climatic conditions, and the negative effect of human disturbances in influencing the location of the colony. Frequently, the aspect of the breeding site has a considerable importance in determining the location of the colony or the location of nests within the colony. For example, Cape Vultures in Lesotho prefer cliffs oriented toward the southeast (which corresponds to northeast in the northern hemisphere) for both nesting and roosting locations, although the cliffs there face north and south in equal proportions (Brown and Piper 1988). Nesting Griffon Vultures most commonly used eastern-facing cliffs in Cyprus (Iezekiel et al. 2004). A long-term study of Egyptian Vultures (*Neophron percnopterus*) in Italy (Liberatori and Penteriani 2001) demonstrated a clear preference of nesting vultures for south-facing cliffs, and exclusive selection of south-facing nest sites within those cliffs. Similarly, sites facing southeast had the greatest probability of nesting by this species in Turkey (Şen 2012).

Aspect preference is also shown by tree-nesting raptors. Short-toed Eagles (*Circaetus gallicus*) in northeastern Greece prefer to build their nests on the south side of the canopy of nest trees, which are situated on south-facing slopes (Bakaloudis et al. 2000, 2001). However, in other regions (as in northwestern Italy), they avoid the south-facing slopes (Bocca 1989). Viñuela and Sunyer (1992) analyzed the influence of nest orientation on hatching success of Black Kites (*Milvus migrans*) in Spain, and found that kites prefer the eastern or southeastern side of the trees, an orientation that increases hatching success.

The Griffon Vulture is a large vulture that feeds exclusively on carrion. Griffon Vultures are gregarious and sociable; they forage in flocks and roost and nest in colonies on steep cliffs in mountainous regions (Cramp and Simmons 1980, Mundy et al. 1992). They are monogamous, and a breeding pair raises a single nestling per year. Incubation period is approximately 55 d, and both sexes incubate, feed, brood, and shade the nestling (Yaniv 2003, Xirouchakis and Mylonas 2007). The young leave the nest at the age of 120–140 d, and continue to receive food from their parents for about 3 mo after fledging, in or near the nest (Yaniv 2003). The species' distribution spans from northern Africa and southwestern Europe in the west to India and Nepal in the east. The largest colonies are in the northern Mediterranean (more than 10,000 breeding pairs in Spain). It is a resident species throughout its distribution range, with records showing dispersal of immature individuals between colonies (Cramp and Simmons 1980). In Israel they are found both in the Mediterranean region and in the desert, and the total number in recent years (1999–2012) ranges between 130 and 460 individuals (33–118 breeding pairs). Until the last decade, a substantial part of the breeding population was concentrated at Gamla canyon in the Golan Heights (Hatzofe 2012).

The population of the Griffon Vulture in Israel has decreased drastically during the last decade, probably as a result of several factors: poisoning (either direct or secondary); persecutions (mostly illegal shooting) and electrocution; food shortage caused by the reduction of foraging areas and increased carcass removal from pastures; nestling mortality either from rickets or from suffocation by swallowing metal fragments, which are brought by the adults with the food to the nest (Court et al. 1997, Yosef and Bahat 2000, Shlosberg and Bahat 2001, Bahat 2002). Another important cause for the reduction of the Griffon Vulture population in Israel is the loss of quality nesting places. Thus, we investigated nest-site characteristics, such as orientation and exposure, which might influence breeding success. More specifically, we examined the relationships among nest-site attractiveness (i.e., how often and how early eggs were laid [a breeding attempt]), the extent of parental time investment, and fledging success.

METHODS

Study Area. Gamla Nature Reserve is situated on the eastern slopes of the Great Rift Valley. The area is mostly characterized by open highland basalt plateau at 400 masl, divided by deep gorges with scattered trees. The reserve consists of a deep canyon (250 m deep) with high cliffs, which contain the majority of the nests. The climate is Mediterranean (maximum average temperature in July: 31.8°C; minimum average temperature in January: 5.9°C; average annual precipitation: 450 mm). The reserve attracts approximately 100,000 visitors annually. In addition, it borders an active military training zone.

Gamla is one of the last nesting and roosting Griffon Vulture colonies left in Israel. During our study, it was the largest colony, with 45–57 nesting pairs, and up to 140 individuals that roosted regularly on the canyon's cliffs.

Data Collection. We studied nest sites and reproduction in Gamla (from 1998 to 2002), in order to relate the physical characteristics of each nest site to the frequency of breeding attempts, their starting date, the hatching success (percentage of eggs that hatched), and the fledging success (percentage of breeding attempts that succeeded in fledging one young). We classified nest sites according to their aspect (facing southeast, southwest or northwest), and according to their exposure: exposed (ledges), semi-covered (partly protected, either by a tree, sidewalls or a partial roof) or covered (small caves). For some calculations, we gave numerical values to the nesting-sites according to their extent of cover, assigning the number 0 to exposed, 0.5 to semi-covered and 1 to covered. Somewhat similar quantitative measures were used by García-Ripollés et al. (2005) to represent climatic variables (such as rainfall, temperature, or hours of daylight) for 10 × 10 km plots in their study of Griffon Vultures in eastern Spain.

We observed thermoregulatory activities of the parents twice a week during the breeding seasons of 2001 and 2002 (a total of 39 and 42 d each season, respectively). We observed from a distance, using a 20–60× telescope. We observed two main thermoregulatory behaviors, brooding and shading. Parents brooded mainly while the nestlings were very young, during the first 2 mo of the nestling phase. Shading started during the first week of the nestling phase and lasted almost until fledging. Thus, we divided the observation period into two phases, the first 2 mo after hatching, and the next 2 mo. We observed at 17 nests in 2001 (of which only nine survived through the second phase), and at 17 nests in 2002 (of which 11 lasted through the second phase). An observation day lasted 6 hr and was divided into 20-min observation sessions. During each session, we recorded the type of adult thermoregulatory activity (brooding or shading) at the observed nest. We defined brooding activity as an adult sitting and covering the nestling with body or wing and shading activity as an adult standing and shading the nestling with body or wing. We calculated the percentage of the 20-min observation sessions during which brooding was observed and the percentage during which shading was observed.

Temperature Measurements. To measure the microclimatic variation among the different types of nest sites, we put two types of data loggers in various nest sites for three different periods: (1) MicroLog data loggers (Fourier Systems Ltd. http://www.fouriersystems.com) during August to early December 2002 (summer and early winter, not part of the breeding season), and (2) Hobo H8 Temp/external data loggers (Onset Computer Corporation, Cape Cod, MA U.S.A.) during March to May 2003 (winter and spring) and during May to early July 2003 (end of spring and summer), both periods within the breeding season. As an index to the overall temperature, we calculated the percentage of time that temperature was >35°C.

Statistical Analyses. We recorded 92 different nest sites in Gamla; that is, sites where eggs were laid at least once during the period 1998–2002. Altogether we recorded 231 breeding attempts in these 92 nest sites. Because we were interested in identifying which nest-site characteristics, such as aspect and exposure, were correlated with breeding success, these 92 nest sites were our units of analysis. Moreover, because the vultures were unmarked,

Table 1. Reproductive performance of Griffon Vultures in Gamla, Israel, during 1998–2002.

YEAR	NUMBER OF EGGS	NUMBER OF HATCHLINGS	NUMBER OF FLEDGLINGS	FLEDGING SUCCESS
1998	33	26	11	33.3%
1999	45	33	17	37.8%
2000	46	30	18	39.1%
2001	57	42	15	26.3%
2002	50	37	17	34.0%
Total	231	168	78	33.8%

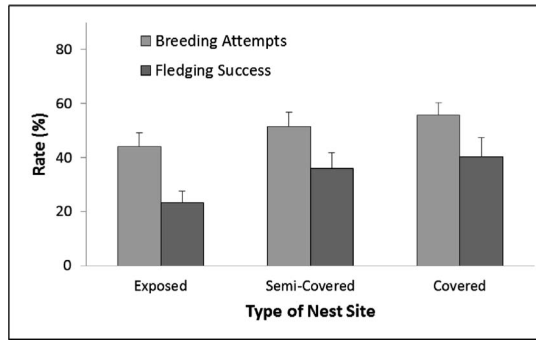

Figure 1. Breeding attempts (per nest site, per year; in %, mean ± SE) and fledging success (in %, mean ± SE), as a function of the extent of cover of the nest sites of Griffon Vultures in Gamla, Israel.

individual identification could not be determined; thus, it was likely that nesting events at the same nest site in different years were not statistically independent. This fact (1) dictated the use of a cluster sampling technique, where the "clusters" are the nest sites, and (2) precluded the comparison of colony performance among different years. The cluster sampling technique (Cochran 1977) was used to estimate the mean and standard error (SE) of hatching success and of fledging success.

We report estimates and standard errors. P values are given for the two-tailed test, unless otherwise stated. When using Wilcoxon's two-sample rank-sum test for data combined from several experiments, the overall P value was calculated by the method suggested in Lehmann (1975). When combining several different t-tests, each performed on a separate data set, but all testing an identical null hypothesis, the overall P value was calculated by the method described in Rosenthal (1978).

RESULTS

Not all 92 nest sites were used with the same frequency: 29 sites were used only once, 21 sites were used twice, 19 were used three times, 12 were used four times, and 11 sites were used in all five years of our study. The mean number of breeding attempts was 0.50 ± 0.03 per site, per year. The mean hatching success (the percentage of breeding attempts in which the egg hatched) was 72.7% ± 3.7%, and the mean fledging success (the percentage of breeding attempts that produced fledging young) was only 33.8% ± 3.6% (Table 1).

We found a significant correlation between the fledging success of a nest site and the frequency of its breeding attempts: nest sites which had a higher fledgling success experienced more breeding attempts (Spearman's rank correlation, $r_s = 0.263$, $n = 92$ and $P = 0.011$). Data on nest initiation dates (the date each breeding attempt started) were available only for 1999–2002. When calculating the correlation between nest occupancy (i.e., the number of times a nest-site experienced a breeding attempt during 1998–2002) and its "attractiveness" (i.e., its rank among the sites with respect to nest initiation date), we found for each year that most frequently used nest-sites were occupied earlier (overall $P = 0.014$). Unsurprisingly, at nests where adults succeeded in fledging their young, breeding attempts started earlier in that year than at nests that failed (Wilcoxon's two-sample rank-sum test, overall $P = 0.012$).

Table 2. Comparison between exposed and covered nest sites of Griffon Vultures in Gamla, Israel (mean ± SE).

	TYPE OF NEST SITE		STATISTIC	
REPRODUCTIVE MEASURE	EXPOSED (n = 29)	COVERED (n = 61)	t	P
Breeding attempts (per site per year)	0.44 ± 0.05	0.54 ± 0.03	$t_{88} = 1.57$	0.12
Hatching success (%)	62.5 ± 6.4	77.4 ± 4.4	$t_{55} = 1.92$	0.06
Fledging success (%)	23.4 ± 4.3	38.4 ± 4.7	$t_{81} = 2.37$	0.02

Mean fledging success at the 31 exposed nest sites was significantly lower ($P = 0.020$) than at the other 61 sites (Table 2). We found no significant correlation between exposure and nest initiation date.

Percentage of breeding attempts per site increased as a function of the degree of cover (linear regression: $r = 0.176$, $n = 90$, and $P = 0.048$; Fig. 1), as well as fledging success (weighted linear regression: $r = 0.198$, $n = 90$, and $P = 0.030$; Fig. 1). Southeast-facing nest sites did not differ from the west-facing (i.e., northwest- and southwest-facing) nest sites in the frequency of breeding attempts, mean hatching success, mean fledging success (Table 3), or nest initiation date.

Temperature Measurements. From August to early December, the microclimate in the northwest-facing aspect was cooler than in the southeast-facing aspect, and caves were cooler than ledges. From March to May, the temperature index did not differ among the nest sites (Fig. 2a). During the third period, May to early July, the caves were cooler than the ledges (Fig. 2b).

Parental Care. Vultures brooded only during the first 2 mo of the nestling phase, when the young were still small, and the environmental temperature can be quite low (we measured a minimum temperature of 4.2°C in March). Brooding activity was higher at unsuccessful nests than at successful nests (Fig. 3), both in 2001 ($t_{15} = 3.438$, $P = 0.004$) and in 2002 ($t_7 = 2.180$, $P = 0.066$), yielding an overall $P < 0.001$.

We expected thermoregulatory activities to be more extensive in less-covered nests. Vultures shaded young during both nestling-rearing phases. The extent of cover of a nest was inversely correlated to the amount of shading by the parents (2001: $r = -0.591$, $n = 9$ and $P = 0.047$; 2002: $r = -0.660$, $n = 11$ and $P = 0.014$; one-tailed tests). Similarly, when considering the total thermoregulatory activity (brooding and shading, during the first nestling phase), we found a negative correlation between the extent of cover of a nest and the amount of thermoregulatory activity by the parents (2001: $r = -0.524$, $n = 17$ and $P = 0.015$; 2002: $r = -0.630$, $n = 17$ and $P = 0.003$; one-tailed tests). Total thermoregulatory activity (during the first nestling phase) was greater on the more exposed southeast-facing cliff than on the northwest-facing cliff ($P = 0.003$ for 2001, and N.S. for 2002, yielding an overall $P = 0.023$; one-tailed tests). However, this can be attributed to the higher percentage of exposed sites on the southeast-facing than on the northwest-facing cliff (36.4% and 26.1%, respectively).

DISCUSSION

Overall, the mean hatching and fledging success of the population of Griffon Vultures at Gamla Nature Reserve were far below the 95% fledging success reported for the same species in Cyprus by Iezekiel et al. (2004) or the 74% fledging success in Crete by Xirouchakis (2010), or the 62.5% fledging success reported by Sarrazin et al. (1996) for the Grand Causses in southern France. Not all the nesting sites of Griffon Vultures in Gamla Nature Reserve had the same frequency of breeding attempts over the years, and we showed that this variability was associated with fledging success and with nest attractiveness—more frequently used sites had higher fledging success, and breeding there started earlier in the season.

We studied the effect of nest type on fledging success, namely the level of protection from above and the aspect of the nest site. Nest sites in caves were more successful and had a higher frequency of breeding attempts than nest sites on open ledges, with semi-covered nest sites (i.e., partly protected, either by a tree, sidewalls, or a partial roof) exhibiting intermediate values. Similar results were

Table 3. Comparison between southeast-facing and west-facing nest sites of Griffon Vultures in Gamla, Israel (mean ± SE).

	FACING OF NEST SITE		STATISTIC	
REPRODUCTIVE MEASURE	SOUTHEAST ($n = 25$)	WEST ($n = 67$)	t	P
Breeding attempts (per site per year)	0.46 ± 0.04	0.52 ± 0.04	$t_{62} = 1.16$	0.25
Hatching success (%)	61.4 ± 8.2	75.9 ± 4.1	$t_{36} = 1.58$	0.12
Fledging success (%)	24.6 ± 5.9	36.8 ± 4.4	$t_{52} = 1.67$	0.10

reported by López-López et al. (2004), who found in their study of Griffon Vultures in eastern Spain that the probability of nest success was lower for nests located on ledges (open or sheltered) than for nests inside caves. Exposure of nesting cliff ledges also had a significant effect on the fledging success of Golden Eagles (*Aquila chrysaetos homeyeri*) in the Israeli Judean and Negev deserts, where less-exposed nests had significantly higher fledging success (Bahat 1991). These differ from a study of Griffon Vultures in northern Spain, where the presence of a rocky shelter had no apparent effect on fledging success (Fernández et al. 1998). They found that high vulture density in the vicinity of the nest (and recent establishment of the site) had significantly negative effects on fledging success, overshadowing any effect of a rocky shelter. Similarly, in eastern Rhodopes, Bulgaria, neither the type of nest-site coverage (cavity or ledge), nor the nest aspect had a significant effect on the fledging success of Griffon Vultures (although pairs breeding in caves had slightly higher fledging success; Demerdzhiev et al. 2014).

Variable microclimatic conditions in different types of nests were also evident from the level of thermoregulatory activities of the parents. As noted

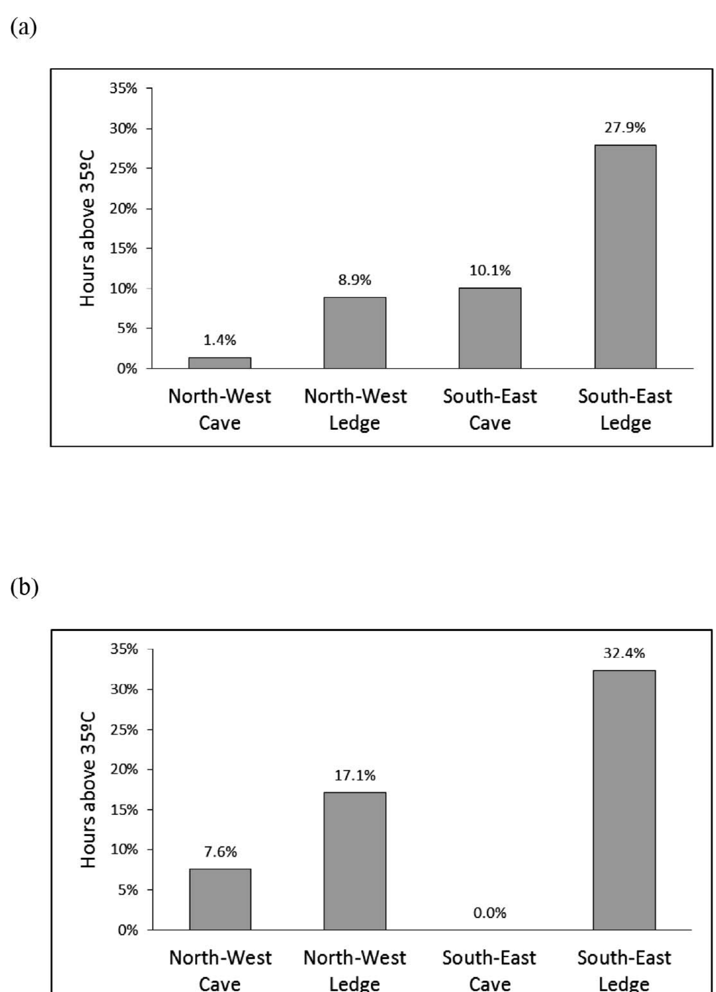

Figure 2. Percent of hours above 35°C (a) during August–early December, (b) during May–early July. During March–May the percentage of hours above 35°C never exceeded 5% in any of the nests.

by Xirouchakis and Mylonas (2007), who studied the breeding behavior of Griffon Vultures in Crete, parent attendance at the nest not only provides protection from predators, but also protects the nestling from inclement weather (mainly rain) and provides shade to prevent the nestling from overheating. In the Pyrenees, Bearded Vultures (*Gypaetus barbatus*) start laying during late December–early March, a period during which temperatures frequently fall below 0°C. The scarcity of appropriate, sheltered nesting cliffs is considered one of the limiting factors of the Bearded Vulture breeding success in that area (Arroyo and Razin 2006).

In our study, parents that were unsuccessful in producing a fledged young, exhibited a higher level of brooding during the first period of the nestling phase. Brooding and shading were more intensive in nests unprotected from above than in sheltered nests, and at southeast-facing cliffs than at northwest-facing cliffs. The latter can be explained by the greater frequency of exposed nest sites on the southeast-facing than on the northwest-facing cliffs.

In studying nesting habitat preferences of Griffon Vultures in eastern Spain, García-Ripollés et al. (2005) considered nesting activity on a scale of 10 × 10 km square sections. They found that occupied squares had significantly lower average temperature in January, and significantly fewer hours of sun during December, than unoccupied squares. It should be emphasized that their study was on a macro-habitat level. In our study, we found a similar preference on the micro-habitat level as well: Griffon Vultures in Gamla preferred the cooler and shadier caves over the exposed ledges as nesting-sites.

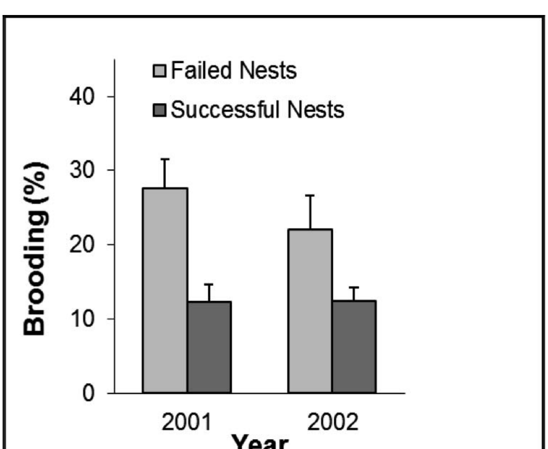

Figure 3. Comparison of brooding activity (percentage of time an adult was sitting and covering the nestling with body or wing) between successful and failed nests of Griffon Vultures in Gamla, Israel.

Nonetheless, we note that nest-site characteristics are not the only factors that influence nesting success. Shortage of carrion can be a possible limiting factor on the growth rate of vulture populations, as shown by Fernández et al. (1998) in a study of a Griffon Vulture population in northern Spain. Gamla, however, is situated among cattle-rich areas, and food is not likely limiting. Poisoning (of adults and nestlings), nestlings suffocating from metal fragments brought by the adults to the nest, electrocution of adults and fledglings, as well as less-suitable nesting sites, were the main reasons for the poor fledging success in Gamla (Court et al. 1997). Density-dependent factors can also have an effect on breeding success in Griffon Vultures; Leconte (1985) and Arroyo et al. (1990) found that medium-size colonies were doing comparatively better than larger or smaller ones in southern France and in Spain.

As a possible management tool, we suggest that an artificial improvement of natural nest sites by making them less exposed (e.g., by digging further into the cliff face after the nesting season) might enhance the nesting conditions and thus the fledging success. This is most crucial where nesting sites are fully exposed and thus have very poor conditions for breeding. A similar procedure increased the breeding success in a Peregrine Falcon (*Falco peregrinus anatum*) aerie in northern California (Pagel 1989): after the nest ledge was enlarged, egg and chick mortality due to falls from the aerie ceased. Nevertheless, such artificial improvements should not minimize the importance of other crucial efforts to reduce poisoning, hunting, and electrocution of the vultures.

Disturbingly, during the last decade, the Griffon Vulture population in Israel has shrunk dramatically (Hatzofe 2012, 2013). Today, only a few dozen pairs are still nesting, mostly in the arid region (the Judean Desert and the Negev Mountains), with only three active nests in Gamla.

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LITERATURE CITED

ARROYO, B., E. FERREIRO, AND V. GARZA. 1990. II Censo Nacional de Buitre Leonado (*Gyps fulvus*): población, distribución, demografia y conservación. ICONA, MAPA, Madrid.

——— AND M. RAZIN. 2006. Effect of human activities on Bearded Vulture behavior and breeding success in the French Pyrenees. *Biological Conservation* 128:276–284.

BAHAT, O. 1991. Choice of directional exposure of Golden Eagle nests in the arid area of Israel. *Israel Journal of Zoology* 37:170–171.

———. 2002. Conservation of threatened raptor populations in Israel. Pages 177–189 *in* Y. Leshem, A. Froneman, P. Mundy, and H. Shamir [EDS.], Wings over Africa. The International Center for the Study of Bird Migration, Tel-Aviv University, Tel Aviv, Israel.

BAKALOUDIS, D.E., C.G. VLACHOS, AND G.J. HOLLOWAY. 2000. Nest features and nest-tree characteristics of Short-toed Eagles (*Circaetus gallicus*) in the Dadia-Lefkimi-Soufli Forest, northeastern Greece. *Journal of Raptor Research* 34:293–298.

———, ———, N. PAPAGEORGIOU, AND G. HOLLOWAY. 2001. Nest-site habitat selected by Short-toed Eagles *Circaetus gallicus* in Dadia forest (northern Greece). *Ibis* 143:391–401.

BOCCA, M. 1989. Status del biancone (*Circaetus gallicus*), del l'aquilla reale (*Aquila chrysaetos*) e del pellegrino (*Falco peregrinus*) in Valle d'Aosta. *Bollettino del Museo Regionale di Scienze Naturali di Torino* 7:163–183.

BROWN, C.J. AND S.E. PIPER. 1988. Status of Cape Vultures in the Natal Drakensberg and their cliff site selection. *Ostrich* 59:126–136.

COCHRAN, W.G. 1977. Sampling techniques. Wiley Press, New York, NY U.S.A.

COURT, L., R. YOSEF, O. BAHAT, AND D. KAPLAN. 1997. Griffon Vulture *Gyps fulvus* nest surveillance project at the Gamla Nature Reserve, Golan Heights, Israel: 1996 conservation report. *Vulture News* 37:10–20.

CRAMP, S. AND K.E.L. SIMMONS. 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.

DEMERDZHIEV, D., H. HRISTOV, D. DOBREV, I. ANGELOV, AND M. KURTEV. 2014. Long-term population status, breeding parameters and limiting factors of the Griffon Vulture (*Gyps fulvus* Hablizl, 1783) population in the Eastern Rhodopes, Bulgaria. *Acta Zoologica Bulgarica* 66:373–384.

FERNÁNDEZ, C., P. AZKONA, AND J.A. DONÁZAR. 1998. Density-dependent effects on productivity in the Griffon Vulture *Gyps fulvus*: the role of interference and habitat heterogeneity. *Ibis* 140:64–69.

GARCÍA-RIPOLLÉS, C., P. LÓPEZ-LÓPEZ, F. GARCÍA-LÓPEZ, J.M. AGUILAR, AND J. VERDEJO. 2005. Modelling nesting habitat preferences of Eurasian Griffon Vulture *Gyps fulvus* in eastern Iberian peninsula. *Ardeola* 52:287–304.

GAVASHELISHVILI, A. AND M.J. MCGRADY. 2006. Breeding site selection by Bearded Vulture (*Gypaetus barbatus*) and Eurasian griffon (*Gyps fulvus*) in the Caucasus. *Animal Conservation* 9:159–170.

HATZOFE, O. 2012. A summary of the Griffon Vulture summer count in Israel, 2012. An internal report, Nature and Parks Authority, Israel (In Hebrew.)

———. 2013. Working with vultures in Israel: conservation, mortality factors, survival, PVA model of the Griffon vultures in Israel and the Middle East. Pages 36–37 *in* C. Papazoglou and C. Charalambous [EDS.], Proceedings of the Griffon Vulture Conference, Limassol, Cyprus.

IEZEKIEL, S., D.E. BAKALOUDIS, AND C.G. VLACHOS. 2004. The status and conservation of Griffon Vulture *Gyps fulvus* in Cyprus. Pages 67–73 *in* R.D. Chancellor and B.-U. Meyburg [EDS.], Raptors worldwide: proceedings of the 6th World Conference on Birds of Prey and Owls, Budapest, Hungary.

LECONTE, M. 1985. Present status of the Griffon Vulture on the northern slopes of the western Pyrenees. *ICBP Technical Publication* 5:117–127.

LEHMANN, E.L. 1975. Nonparametrics: statistical methods based on ranks. Holden-Day, San Francisco, CA U.S.A.

LIBERATORI, F. AND V. PENTERIANI. 2001. A long–term analysis of the declining population of the Egyptian Vulture in the Italian peninsula: distribution, habitat preference, productivity, and conservation implications. *Biological Conservation* 101:381–389.

LÓPEZ-LÓPEZ, P., C. GARCÍA-RIPOLLÉS, AND J. VERDEJO. 2004. Population status and reproductive performance of Eurasian Griffons (*Gyps fulvus*) in eastern Spain. *Journal of Raptor Research* 38:350–356.

MARGALIDA, A., D. GARCÍA, AND A. CORTÉS-AVIZANDA. 2007. Factors influencing the breeding density of Bearded Vultures, Egyptian Vultures and Eurasian Griffon Vultures in Catalonia (NE Spain): management implications. *Animal Biodiversity and Conservation* 30:189–200.

MONSARRAT, S., S. BENHAMOU, F. SARRAZIN, C. BESSA-GOMES, W. BOUTEN, AND O. DURIEZ. 2013. How predictability of feeding patches affects home range and foraging habitat selection in avian social scavengers? *PLoS ONE* 81: e53077. doi:10.1371/journal.pone.0053077 (last accessed 28 December 2016).

MUNDY, P., D. BUTCHART, J. LEDGER, AND S. PIPER. 1992. The vultures of Africa. Acorn Books and Russel Friedman Books, Randburg, South Africa.

NEWTON, I. 1979. Population ecology of raptors. T. and A.D. Poyser, Berkhamsted, U.K.

PAGEL, J.E. 1989. Use of explosives to enhance a Peregrine Falcon eyrie. *Journal of Raptor Research* 23:176–178.

ROSENTHAL, R. 1978. Combining results of independent studies. *Psychological Bulletin* 85:185–193.

SARRAZIN, F., C. BAGNOLINI, J.L. PINNA, AND E. DANCHIN. 1996. Breeding biology during establishment of a reintroduced Griffon Vulture *Gyps fulvus* population. *Ibis* 138:315–325.

ŞEN, B. 2012. Breeding ecology of the Egyptian Vulture (*Neophron percnopterus*) population in Beypazari. Ph.D. dissertation, Middle East Technical University, Ankara, Turkey.

SHLOSBERG, A. AND O. BAHAT. 2001. The risks of toxicoses from pesticides and pollutants in raptors and wildlife in Israel – the present situation and recommendations for the future. Society for the Protection of Nature in Israel, Tel Aviv, Israel.

VIÑUELA, J. AND C. SUNYER. 1992. Nest orientation and hatching success of Black Kites *Milvus migrans* in Spain. *Ibis* 134:340–345.

XIROUCHAKIS, S.M. 2010. Breeding biology and reproductive performance of Griffon Vultures *Gyps fulvus* on the island of Crete (Greece). *Bird Study* 57:213–225.

——— AND M. MYLONAS. 2005. Selection of breeding cliffs by Griffon Vultures *Gyps fulvus* in Crete (Greece). *Acta Ornithologica* 40:155–161.

——— AND ——— 2007. Breeding behaviour and parental care in the Griffon Vulture *Gyps fulvus* on the island of Crete (Greece). *Ethology Ecology & Evolution* 19:1–26.

YANIV, S. 2003. The division of parental care between the sexes in the Griffon Vulture (*Gyps fulvus*). M.Sc. thesis, The Hebrew University of Jerusalem, Jerusalem, Israel (In Hebrew.)

YOSEF, R. AND O. BAHAT. 2000. Habitat loss and vultures: a case study from Israel. Pages 207–212 *in* R.D. Chancellor and B.-U. Meyburg [EDS.], Raptors at risk: proceedings of the 5th World Conference on Birds of Prey and Owls, Midrand, South Africa.

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