Israel Journal of Ecology & Evolution, 2017
http://dx.doi.org/10.1163/22244662-06301007

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Nest-Site Fidelity in Griffon Vultures: A Case of Win–Stay/Lose–Shift?

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Abstract We studied the use of nest-sites by Griffon Vultures (*Gyps fulvus*) and the breeding success in these sites during 1998–2002 in Gamla Nature Reserve (Israel). Nest-sites in which a breeding attempt succeeded in fledging a young, were more likely to be occupied by nesting vultures in the following breeding season, than nest-sites that experienced a failure. This suggests that Griffon Vultures in Gamla used a Win–Stay/Lose–Shift strategy regarding nest-site fidelity.

Keywords: Griffon Vulture; *Gyps fulvus*; nest-site fidelity; Win–Stay/Lose–Shift; breeding success; nesting success

Introduction

Win–Stay/Lose–Shift (*syn.* Win–Stay/Lose–Switch, WSLS) is a well-documented strategy in animal behavior, particularly in the context of optimal foraging. An individual adopting the WSLS strategy tends to stick to its present state as long as the reward it obtains is substantial enough, and to alter its state after disappointments. For example, in a patchy environment in which patchiness is concealed, if a WSLS forager is rewarded, it tends to stay close, and if not, it tends to shift to another area [hence the term near–far search as suggested by Selten & Shmida (1991) in foraging theory]. WSLS has been shown to be an optimal strategy if food distribution is patchy (Hodges 1985), but in some situations it is evolutionarily stable also under a uniform distribution (Motro & Shmida 1995). Examples for WSLS foraging are numerous – bees foraging for nectar (Heinrich 1979; Waddington 1980, 1983; Dukas & Real 1993; Keasar et al. 1996), birds (Smith 1974, Gill & Wolf 1977, Zach & Falls 1977), mammals (Mendl et al. 1997) and many more.

WSLS behavior has also been extensively documented with respect to nest-site fidelity. Nolan (1978) reports that among the 34 surviving females of Prairie Warbler (*Dendroica discolor*) that experienced nest success, 47% returned on the subsequent year to the same nesting area, compared to only 17% for surviving females that failed. Shields (1984) found a higher tendency to "divorce" after nesting failure than after success, for both sexes in the Barn Swallow (*Hirundo rustica*). Weatherhead & Boak (1986) demonstrated a strong WSLS behavior of Song Sparrow (*Melospiza melodia*) males towards their nesting territory. Bobolinks (*Dolichonyx oryzivorus*) display a resource-dependent WSLS behavior – it is stronger in a poor habitat than in a rich one (Bollinger & Gavin 1989). Female Red-winged Blackbirds (*Agelaius phoeniceus*) moved significantly farther if their last nest on the previous year was unsuccessful (Beletsky & Orians 1991). Beheler et al. (2003) show a marked WSLS behavior for both males and females of Eastern Phoebes (*Sayornis phoebe*) in successive nesting within the same year, but not between years. The within-season re-nesting behavior of the multi-brooded Brewer's Sparrow (*Spizella breweri*) demonstrates the use of a WSLS strategy: Pairs moved sequential nest sites slightly farther following nest predation versus success, and changed nest patch attributes associated with probability of nest predation to a greater extent following nest predation than success (Chalfoun & Martin 2010). The use of *public information* by individual birds with regard to their local migration decisions was demonstrated by Doligez et al. (2002) in their experimental study of wild Collared Flycatchers (*Ficedula albicollis*). Birds monitor the current reproductive success of others, and their probability of emigration increased both when local offspring quantity or quality decreased.

In his extensive study on the breeding ecology of female Sparrowhawks (*Accipiter nisus*) in Scotland, Newton (1993) reported that 83% of 251 females that experienced nest success, stayed on the same territory for their next breeding, whereas this percentage was only 39% among the 82 females that failed. Forero et al. (1999) report that breeding failure and mate loss (divorce or death) favored breeding dispersion, both in males and females of Black Kites (*Milvus migrans*). In their study of breeding dispersal in the colonial Lesser Kestrel (*Falco naumanni*), Calabuig et al. (2008) conclude that dispersal may result in part from a negative perception of the quality of the colony of

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origin affected by a bad breeding experience in the previous season. Using Steenhof & Peterson (2009) data on American Kestrels (*Falco sparverius*) nesting in boxes in southwestern Idaho, a significant WSLS behavior is evident for both males ($p = 0.022$) and females ($p = 0.001$).

In this work we document WSLS behavior with regard to nest-site fidelity of Griffon Vultures (*Gyps fulvus*) in northern Israel. Our hypothesis is that successful breeding in a nest site would enhance its chances to be occupied in the next season, whereas failure will enhance its desertion.

Methods

The Griffon Vulture

The Griffon Vulture is a large vulture that feeds exclusively on carrion. Based on the unpredictable nature of their food resources, Griffon Vultures are gregarious and sociable; they forage in flocks and roost and nest in colonies on steep cliffs in mountainous regions (Cramp & 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 & 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. The species' distribution spans from northern Africa and southwestern Europe in the west to India and Tibet in the east. The largest colonies are in the northern Mediterranean (more than 24,000 breeding pairs in Spain, Del Moral 2009). It is a resident species throughout its distribution range, with records showing dispersal of immature individuals between colonies (Cramp & Simmons 1980), as well as daily short-range movements and seasonal long-range movements of individuals of all age groups (Bahat et al. 1993; Bahat 1995; 1997; Spiegel et al. 2015). 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 (33–144 breeding pairs). Until the last decade, a substantial part of the breeding population was concentrated at Gamla Nature Reserve in the Golan Heights (Court et al. 1997, Becker et al. 2005, Hatzofe 2012).

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 m height above sea level, 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 vulture 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. During our study, Gamla was the largest Griffon Vulture colony in Israel, 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 Nature Reserve 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 and the fledging success (Freund et al. 2017). A nest-site was defined as a niche – either a small cave, or a partly protected (by a tree, sidewalls or a partial roof) ledge or an exposed ledge – in which at least once during the years of our study, an egg laying event was recorded. Not all nest-sites are used with the same frequency, and the mean number of nesting events was 0.502 per niche, per year. The mean fledging rate (the percentage of egg laying events that produced fledging young) was only 33.77%. Using the same data set, we analyze here the relationship between the success or failure of a breeding attempt in a site, and the use of this site by any vultures for breeding in the following year. We define as success any breeding attempt that succeeded in fledging a young. Hence, our units of sampling are the nesting sites that have experienced at least one breeding attempt during 1998–2001. We have chosen this approach since the vultures in our study were not tagged or marked, thus individual identification was impossible. So instead of analyzing WSLS from the individual's perspective, according to its own experience, we try here to deduce WSLS from the colony's perspective – how do individuals in the colony, using public information, react towards a nest-site that during the previous breeding season, the nesting attempt in it ended in a success or a failure.

Each breeding attempt creates a "chain-link" between its outcome (success or failure) and the use of that nest site in the next year (occupied or unoccupied). Thus, we can distinguish four types of chain-links: Success–Occupied, Success–Unoccupied, Failure–Occupied and Failure–Unoccupied (quite analogous to Win–Stay, Win–Shift, Lose–Stay and Lose–Shift in game theory terminology). Note that each nest site can have between 1 to 4 such chain-links.

Statistical Analysis and Results

94 nest sites in Gamla canyon and adjacent tributaries have experienced at least one breeding attempt during 1998–2001: 41 had only one chain-link, 29 had two, 13 had three, and 11 nest sites had four chain-links (i.e., were occupied in all five years of our study), thus the total number of chain-links was 182 (see Appendix). Note that chain-links that belong to the same nest-site are not independent, because of possible nest-site fidelity by specific vultures. In addition, we expect better nest-sites to be occupied more often (Freund et al. 2017), and as a result to contain more chain-links. Therefore, we can either randomly choose only one chain-link from each nest-site, or analyze each year separately. Also note that our hypothesis is one-sided, thus we are considering the one-tailed p-value.

Randomly choosing only one chain-link from each nest-site: We repeated this procedure 10^4 times. At each iteration, we calculated the square root of the chi-square statistic for independence, and the one-tailed p-value of our one-sided alternative (using the fact that the square root

Table 1. Number of occupied and unoccupied nest-sites in the years 1999–2002, that have been occupied in the previous year. The data is divided between nest-sites that in the previous year succeeded in fledging a young (Success), and nest-sites that failed (Failure). The last line presents the one-tailed significance of the Fisher's exact test.

	1999		2000		2001		2002	
	Occupied	Unoccupied	Occupied	Unoccupied	Occupied	Unoccupied	Occupied	Unoccupied
Success	8 (67.7%)	4 (33.3%)	8 (47.1%)	9 (52.9%)	14 (93.3%)	1 (6.7%)	12 (75.0%)	4 (25.0%)
Failure	13 (61.9%)	8 (38.1%)	14 (43.8%)	18 (56.3%)	13 (54.2%)	11 (45.8%)	20 (44.4%)	25 (55.6%)
	N.S.		N.S.		$p = 0.010$		$p = 0.034$	

of the chi-square variable with one degree of freedom has the standard normal distribution). The mean of these 10^4 chi-square statistics was 4.932, and the mean one-tailed p-value was 0.037, implying that successful breeding in a nest site enhanced its chances to be occupied in the next season, while failure enhanced its desertion.

Analyzing each year separately: For each of the four years (1999–2002), the percentage of "Occupied" among the nest-sites that succeeded in fledging a young in the previous breeding season is larger than the percentage of "Occupied" among the nest-sites that failed. However, only for two years the one-tailed Fisher's exact test yielded a significant result (Table 1).

Discussion

We studied Griffon Vultures' conditional nest site fidelity, i.e., fidelity that depends on the outcome of the previous nesting attempt in that site. In particular, we were interested in examining whether individual vultures are practicing a Win–Stay/Lose–Shift strategy towards their nest-sites. For that purpose, we used observations on nesting dynamics in Gamla Nature Reserve in northern Israel, collected during 1998–2002. Altogether, we had 94 nest-sites that experienced at least one breeding attempt during 1998–2001. The vultures in this study were neither tagged nor marked in any way, thus individual identification was not possible. Our approach was intentionally non-invasive – the population of Griffon Vultures in Israel is in an endangered state, and we refrained from disturbing it by capturing and tagging. A precise study of WSLS on the individual level requires an individual identification. Hence we cannot give an absolute answer to the question as to what extent the Griffon Vultures are applying WSLS strategy towards their choice of nest-sites. Instead, we chose to study the Success–Occupied/Failure–Unoccupied occurrences in the nest-sites, which are suggestive, yet not fully indicative of the individuals' behavior (e.g., theoretically one cannot distinguish between a "Stay" of the former resident, or a "Shift" and occupation by other individuals). Our results support the Success–Occupied/Failure–Unoccupied phenomenon, and indirectly support the fact that Griffon Vultures are actually performing a Win–Stay/Lose–Shift behavior. A future research, based on individual identification, should be conducted in order to confirm the apparent WSLS behavior of the vultures. Nevertheless, we should be aware to the risk of human interference in nesting colonies of Griffon Vultures, especially if the number of suitable nest-sites is a limiting factor. Human interference that results in a real, or even in an apparent, nesting failure can lead to an abandonment of this site in consecutive seasons.

Disturbingly, during the last decade, the Griffon Vulture population in Israel has shrunk dramatically (Hatzofe 2012, 2013). Today, only a few dozens of pairs are still nesting, mostly in the arid region (the Judean Desert and the Negev Mountains). While most of the individuals in Israel are equipped now with identification means, only three active nests were still left in Gamla last year, and none succeeded to fledge any young.

Acknowledgements

We thank Gil Ben-Noon, the Director of Gamla Nature Reserve during our study period, for his invaluable help in the field; Shmulik Hershkowitz and the late Orna Eshed for their help in accessing previous databases of Gamla.

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Appendix

Nest-Site	Success 1998	Occupied 1999	Success 1999	Occupied 2000	Success 2000	Occupied 2001	Success 2001	Occupied 2002
Abba							Yes	Yes
Amit					Yes	Yes	No	No
Amnon	Yes	No						
Anna			No	No				
Avishai							No	No
Avshalom	No	No					No	Yes
Balcony	No	Yes	No	No			Yes	Yes
Big Cave	No	No					Yes	No
Black Cliff	No	Yes	Yes	Yes	Yes	Yes	No	Yes
Blues			No	No			No	No
Cuckoo	No	Yes	No	Yes	Yes	No		
Dedi							No	No
Dracula					No	No		
Dragon					No	Yes	No	No
Egyptian Hole			Yes	No			Yes	Yes
Eitan			Yes	No			No	No
Elal							Yes	Yes
Esav			Yes	Yes	Yes	Yes	Yes	Yes
Etzilly			No	Yes	No	Yes	No	No
Fox			No	Yes	No	Yes	No	Yes
Gershon			No	No				
Ginger	Yes	Yes	Yes	No				
Greenie							No	No
Gulo					No	No		
Hassan	Yes	Yes	No	Yes	No	Yes	No	Yes

Nest-Site	Success 1998	Occupied 1999	Success 1999	Occupied 2000	Success 2000	Occupied 2001	Success 2001	Occupied 2002
Hermit	No	No						
Iris			No	No				
Ivan	Yes	No					No	No
Jesus							No	No
Kida 1							No	Yes
Kida 2							No	No
Klomp 1			No	Yes	No	No		
Klomp 2					No	No		
Life			No	Yes	Yes	Yes	No	No
Mercy			No	No			Yes	Yes
Mint	Yes	No						
Mody			Yes	Yes	Yes	Yes	No	No
Mooz					No	No		
Namer					No	Yes	Yes	Yes
Navale							No	No
Neil Young							Yes	No
New Black Cliff	No	Yes	Yes	Yes	Yes	Yes	No	No
No Name	No	Yes	No	Yes	Yes	Yes	No	Yes
Oli							No	Yes
Pole					No	Yes	No	Yes
Princess Yes					No	No		
Princess 2					No	No		
Quarry 1							Yes	No
Quarry 2					Yes	Yes	No	Yes
R	Yes	Yes	No	Yes	No	Yes	No	Yes
Rachel							Yes	Yes
Scully			No	Yes	No	Yes	No	Yes
Shady	No	No						
Shaul 1			No	No			No	Yes
Shaul 2			No	No				
Sheba			Yes	No				
Shmulick 1	No	Yes	No	Yes	Yes	Yes	No	No
Shmulick 2	No	Yes	No	No				
Shy			No	No				
Silvi							Yes	Yes
Sisra			No	No			Yes	No
Spits 1	Yes	No						
Spits 2a	No	Yes	No	Yes	Yes	Yes	Yes	Yes
Spits 2b	No	Yes	No	No				
Spits 3	Yes	Yes	No	No			No	Yes
Spits 4	No	Yes	Yes	Yes	Yes	Yes	No	No
Stalona A	No	Yes	Yes	No				
Stine	No	No			Yes	Yes	No	Yes
Tamar	No	No						
Titus	No	No			No	No		
Toda					No	Yes	No	No
Top 1	Yes	Yes	Yes	No				
Top 2			Yes	No				
Triangle Hole	No	No						
Trio East	No	Yes	Yes	Yes	No	No		
Trio West					No	No		
Tsilla			No	Yes	No	No		
Tuval							No	No
War			No	No			Yes	Yes
Yael			Yes	No			No	Yes
Yair 1			No	No			No	No
Yair 2			No	No				
Yarden			No	No			No	No
Yofi 1					No	Yes	No	No
Yofi 2							No	No
Yoheved							No	No
Yona			Yes	Yes	No	Yes	No	Yes
Yotam 1	No	Yes	No	Yes	Yes	Yes	No	Yes
Yotam 2	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Yotam 3	Yes	Yes	Yes	No			No	Yes
Yotam 4a	Yes	Yes	No	Yes	No	Yes	No	Yes
Yotam 4b			No	No				
Zeresh 1					No	Yes	No	Yes
Zeresh 2							No	No