

Nest-site fidelity in Lesser Kestrels: a case of Win–Stay/Lose–Shift?

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

^aDepartment of Ecology, Evolution and Behavior, The Hebrew University of Jerusalem, Jerusalem 91904, Israel

^bMitrani Department of Desert Ecology, Blaustein Institute for Desert Research, Ben Gurion University of the Negev, Sde Boker Campus 84990, Israel

^cDepartment of Ecology, Evolution and Behavior, Department of Statistics, and The Federmann Center for the Study of Rationality, The Hebrew University of Jerusalem, Jerusalem 91904, Israel

Abstract We studied Lesser Kestrels' (*Falco naumanni*) 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 kestrels practice a Win–Stay/Lose–Shift (WSLS) strategy towards their nest-sites; that is, does the tendency to use the same nest-site increase following a successful nesting season, but decrease following a failure. For that purpose, we documented the use of nest-sites by Lesser Kestrels and the breeding success in these sites during 1998–2003 in the city of Jerusalem (Israel). We found that while Lesser Kestrels do not practice WSLS strategy towards their nest-site, the males (but not the females) do so towards their sub-colony – they tend to stay in the same sub-colony if their nesting was successful, whereas they tend to migrate to a different sub-colony after failure. A possible explanation to this sexual difference in WSLS behavior can arise from the fact that changing a sub-colony entails a change of hunting area. The male, being the main food provider in the Lesser Kestrel, may be more sensitive to this opportunity.

Keywords Lesser Kestrel; *Falco naumanni*; 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 current state (e.g., foraging patch, prey type, flower type etc.) as long as the reward it obtains is substantial enough, and to alter its state after disappointments.

WSLS behavior has also been extensively documented with respect to nest-site fidelity. This behavior is important for understanding factors that underlay decision-making in relation to nest site selection, specifically factors that may lead to abandoning a nest versus reusing it. Nolan (1978) reported 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 and Boak (1986) demonstrated a WSLS behavior of Song Sparrow (*Melospiza melodia*) 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 and Gavin 1989). Female Red-winged Blackbirds (*Agelaius phoeniceus*) moved significantly farther if their last nest on the previous year was unsuccessful (Beletsky and Orians 1991). In his extensive study on the breeding ecology of female

European 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) reported that breeding failure and mate loss (divorce or death) favored breeding dispersion, both in males and females of Black Kites (*Milvus migrans*). Doligez et al. (2002) demonstrated that wild Collared Flycatchers (*Ficedula albicollis*) use public information of the breeding success of other individuals with regard to their migration decisions. In their experimental study, the birds monitored the current reproductive success of others, and their probability of emigration increased both when local offspring quantity or quality decreased. Beheler et al. (2003) showed a marked WSLS behavior for both males and females of Eastern Phoebe (*Sayornis phoebe*) in successive nesting within the same year, but not between years. In their study of breeding dispersal in the colonial Lesser Kestrel (*Falco naumanni*), Calabuig et al. (2008) concluded that dispersal may result in part from a negative perception of the quality of the colony of origin affected by a bad breeding experience in the previous season. Although not explicitly stated, Steenhof and Peterson (2009) data on American Kestrels (*Falco sparverius*) nesting in boxes in southwestern Idaho provide evidence for a significant WSLS behavior in both males and females (based on our analysis of their nesting data). The within-season re-nesting behavior of the multi-brooded Brewer's Sparrow (*Spizella breweri*) demonstrates

*Corresponding author. E-mail: msumotro@mail.huji.ac.il

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 and Martin, 2010). Freund et al. (2017) documented WSLs behavior with regard to nest-site fidelity of Griffon Vultures (*Gyps fulvus*) in northern Israel – successful breeding in a nest site enhances its chances to be occupied in the next season, whereas failure enhances its desertion.

All these examples confirm the reasonable presumption that after an unsuccessful breeding event, a parent will tend to avoid some of the factors that may be responsible of that failure, by shifting to a different nesting location. These factors include micro and macro climatic conditions, predation pressure, food shortage, human disturbances, unfit partner, etc. Some of these factors can be changed by shifting to a nearby nest location, if available, and some – like changing foraging or hunting areas – require a more substantial change.

In this work, we explore WSLs nesting behavior of Lesser Kestrels in an urban colony in Jerusalem, Israel. The colony is divided into several sub-colonies, which are separated from each other by several hundred meters to a few kilometers. Individuals of each sub-colony hunt together, each sub-colony in its distinct hunting areas. Being a part of a larger, multi-aspect study of this colony, each nest in our present work has already been identified by its sub-colony and its specific site within the sub-colony.

Methods

Study species

The Lesser Kestrel (*Falco naumanni*) 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 region and western and central Asia, and wintering mainly in sub-Saharan Africa. In Israel, the Lesser Kestrel is a summer breeding visitor, arriving during the second half of February, and nesting usually terminates in early June. Clutch size is usually 3–5 eggs and both parents take turns incubating for ca. 1 month (Liven-Schulman et al., 2004; Iñigo and Barov, 2011). Lesser Kestrels feed almost exclusively on arthropods, mainly of the Coleoptera, Orthoptera and Solifugae orders, but also on reptiles and rodents (Kopij and Liven-Schulman, 2012). They exhibit sexual dimorphism, both in plumage colors and in size – the females are larger than the males. In Israel, the estimated weights (mean \pm sd, in gr.) are 139.1 ± 15.8 ($n = 110$) and 128.5 ± 10.8 ($n = 158$) for females and males, respectively (A. Gal, personal observations).

Study area

We studied the colony of Lesser Kestrels in Jerusalem, Israel. The kestrels nest in several neighborhoods in the

city, in sub-colonies which are separated from each other by several hundred meters to a few kilometers. Within each sub-colony, nests are located in the same building or in adjacent buildings of that neighborhood. Individuals of each sub-colony hunt together, each sub-colony in its distinct hunting areas (O. Bobek, personal observations). During the study period (1998–2003), the Lesser Kestrel colony in Jerusalem (Israel) decreased from 60–80 nesting pairs in 1998–1999 (Schulman 2001) to 40 pairs in 2003.

Data collection

We documented nest-site occupancy and breeding success from 1998 to 2003. The breeding individuals were all marked, so we could trace the nesting location of each kestrel during the years of its breeding. For the Win–Stay/Lose–Shift analysis, we considered only those individuals for which we have at least one ‘chain-link’, that is – data on the nesting location in two consecutive years, together with the nesting success (yes or no) in the first year. Thus, we can distinguish four types of chain-links: success–stay, success–shift, failure–stay and failure–shift (analogous to win–stay, win–shift, lose–stay and lose–shift in game theory terminology).

Statistical analysis and results

Altogether, we collected data on 39 individuals that had at least one chain-link – 15 females and 24 males – and the number of chain-links per individual ranges between 1 and 3. Twenty three individuals had only one chain-link, 11 had two, and 5 had three chain-links, thus the total number of chain-links was 60 (see Table 1). Note that chain-links that belong to the same individual are not independent, therefore we had to randomly choose only one chain-link from each individual.

First, we estimated the unconditional fidelity of the breeding kestrels to their nest (i.e., the probability that a breeding individual will stay and breed in the same nest for the next year, irrespective of the outcome of its present breeding). This can easily be derived from Table 1.

There are $1^{23} \times 2^{11} \times 3^5 = 497,664$ different possibilities of choosing only one chain-link from each of the 39 individuals, and we used a bootstrapping technique for the WSLs analysis. Thus, we randomly sampled 10^4 of these possibilities. For each sampled possibility, after choosing the 39 chain-links, we calculated the square root of the chi-square statistic for independence between success/failure and stay/shift, and the its p -value (using the fact that the square root of the chi-square variable with one degree of freedom has the standard normal distribution). Note that our WSLs hypothesis is one-sided, therefore we are considering the one-tailed p -value. Thus, we obtained 10^4 chi-square statistics, each with its corresponding p -value. Finally, we calculated the mean of these 10^4 chi-square statistics and the mean of the p -values.

A similar procedure was applied for analyzing the sub-colony fidelity.

Table 1. Nest-site occupancy and breeding success. Each line corresponds to a different individual. Nests are identified by a letter (which denotes the sub-colony) followed by a number (which distinguishes the nest within the sub-colony). To the right of each nest is the number of fledglings. The three right-most columns give the number of chain-links (see text) and the proportions of nest-site and sub-colony fidelity for each individual.

| ID | Sex | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | Chain-links | Nest-site Fidelity | Sub-colony Fidelity |
|-------|-----|------|------|------|--------|------|------|-------------|--------------------|---------------------|
| 13181 | F | | R6 | R4 | 1 | | | 1 | 0.000 | 1.000 |
| 13199 | F | | B4 | N2 | 0 | | N5 | 3 | 0.000 | 0.667 |
| 13325 | F | | M32 | M5 | 1 or 2 | | M5 | 3 | 0.667 | 1.000 |
| 14562 | F | | | M20 | 2 | | N8 | 2 | 0.500 | 0.500 |
| 15133 | F | | | | | | K8 | 1 | 0.000 | 0.000 |
| 15416 | F | M14 | 2 | R3 | 1 | | R4 | 3 | 0.333 | 0.667 |
| 15418 | F | | | K25 | 2 | | K4 | 2 | 0.000 | 1.000 |
| 15439 | F | | | N7 | 1 | | N8 | 1 | 0.000 | 1.000 |
| 15448 | F | | | R1 | 0 | | R1 | 1 | 1.000 | 1.000 |
| 15469 | F | | | | | | K10 | 1 | 0.000 | 0.000 |
| 16509 | F | | R4 | H5 | 0 | | HI | 2 | 0.000 | 0.500 |
| 16514 | F | | | M6 | 2 | | M30 | 1 | 0.000 | 1.000 |
| 16521 | F | | | | | | M35 | 1 | 0.000 | 1.000 |
| 16540 | F | | | M7 | 1 or 2 | | M6 | 2 | 0.500 | 1.000 |
| 16549 | F | | | | | | M48 | 1 | 0.000 | 1.000 |
| 10184 | M | | | N6 | 2 | | N6 | 2 | 0.500 | 1.000 |
| 10188 | M | M22 | 2 | M7 | 1 or 2 | | M7 | 3 | 0.667 | 1.000 |
| 10196 | M | | | N8 | 2 | | | 1 | 0.000 | 0.000 |
| 10198 | M | | | A4 | 3 | | | 1 | 0.000 | 0.000 |
| 13153 | M | A3 | 1 | HI | 2 | | | 2 | 0.000 | 0.500 |
| 13168 | M | J11 | 0 | | | | | 1 | 0.000 | 1.000 |
| 13170 | M | | | J15 | 0 | | | 1 | 1.000 | 1.000 |
| 13173 | M | M24 | 2 | M47 | 3 | | M24 | 3 | 0.000 | 1.000 |
| 13179 | M | M35 | 2 | | | | | 1 | 0.000 | 1.000 |
| 13189 | M | | | H5 | 0 | | N7 | 1 | 0.000 | 0.000 |
| 13193 | M | A6 | 0 | | | | | 1 | 0.000 | 0.000 |
| 13203 | M | N2 | 2 | | | | | 1 | 0.000 | 1.000 |
| 14594 | M | | | K22 | 3 | | K12 | 2 | 0.000 | 1.000 |
| 15407 | M | | | K16 | 4 | | K8 | 2 | 0.000 | 1.000 |
| 15409 | M | | | K10 | 2 | | | 2 | 0.000 | 0.000 |
| 15450 | M | | | M11 | 1 or 2 | | M11 | 1 | 1.000 | 1.000 |
| 15451 | M | | | | | | M24 | 2 | 0.000 | 1.000 |
| 15453 | M | | | N3 | 1 | | | 1 | 0.000 | 0.000 |
| 15468 | M | M27 | 3 | M8 | 2 | | | 2 | 0.000 | 1.000 |
| 15473 | M | | | M19 | 0 | | | 1 | 0.000 | 0.000 |
| 15493 | M | | | | | | M35 | 1 | 0.000 | 0.000 |
| 16502 | M | | | | | | M24 | 3 | 1.000 | 1.000 |
| 16542 | M | | | R4 | 2 | | HI | 1 | 0.000 | 0.000 |
| 16560 | M | | | | | | M34 | 2 | 0.000 | 1.000 |

Table 2. Nest-site and sub-colony fidelity. Each cell presents the conditional percentage of stay and shift, given nesting success or nesting failure.

| | Nest-site Fidelity | | | Sub-colony Fidelity | |
|---------|--------------------|-------|---------|---------------------|-------|
| | Stay | Shift | | Stay | Shift |
| Success | 22.3% | 77.7% | Success | 75.3% | 24.7% |
| Failure | 8.8% | 91.2% | Failure | 44.1% | 55.9% |

Nest-site fidelity

The estimate of the unconditional fidelity of the breeding kestrels to their nest was 0.184 ± 0.055 (mean \pm se). Separating females from males, we get 0.200 and 0.174 as estimates for females and males, respectively, and a non-significant difference between the sexes (Mann-Whitney $U = 164$, p -value = 0.612).

Next, addressing the WSLS behavior, successful breeding in a nest-site increased the probability of the breeding individual to stay in this site for the consecutive year from 0.184 to 0.223, and failure increased the probability of shifting to a different nest-site from 0.816 to 0.912 (Table 2). However, these results are not statistically significant – using the above-mentioned bootstrapping method, the mean of the 10^4 chi-square statistics was 0.972, and the mean one-tailed p -value was 0.174. Analyzing each sex separately, we find that WSLS regarding nests does not exist neither in females (mean chi-square = 0.259, mean p -value = 0.604, 10^4 iterations), nor in males (mean chi-square = 2.073, mean p -value = 0.078, 10^4 iterations).

Sub-colony fidelity

The estimate of the unconditional fidelity of the breeding kestrels to their sub-colony (i.e., the probability that a breeding individual will stay and breed in the same sub-colony for the next year, irrespective of the outcome of its present breeding), was 0.662 ± 0.071 (mean \pm se). Separating females from males, we get 0.756 and 0.604 for females and males, respectively, and a non-significant difference between the sexes (Mann-Whitney $U = 159$, p -value = 0.476).

Addressing the WSLS behavior, successful breeding in a nest-site increased the probability of the breeding individual to stay in the same sub-colony for the consecutive year from 0.662 to 0.753, and failure increased the probability of shifting to a different sub-colony from 0.338 to 0.559 (Table 2). These results are statistically significant – using the above-mentioned bootstrapping method, the mean of the 10^4 chi-square statistics was 3.755, and the mean one-tailed p -value was 0.046. Thus, the Lesser Kestrels of Jerusalem display a WSLS behavior towards sub-colony, that is, successful breeding in a nest-site increases the probability of the breeding individual to stay in the same sub-colony for the consecutive year, and failure increases its probability of moving to a different sub-colony. Analyzing each sex separately, we find that WSLS regarding sub-colony does not exist in females (mean chi-square = 0.730, mean p -value = 0.404, 10^4 iterations), whereas it

significantly exists in males (mean chi-square = 4.398, mean p -value = 0.026, 10^4 iterations).

Discussion

We studied Lesser Kestrels' 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 kestrels are practicing a Win–Stay/Lose–Shift strategy towards their nest-sites. For that purpose, we used observations on nesting dynamics in the city of Jerusalem (Israel), collected during 1998–2003. It turns out that while lesser kestrels do not practice WSLS strategy towards their nest-site, the males (but not the females) do so towards their sub-colony – they tend to stay in the same sub-colony if their nesting was successful, whereas they tend to migrate to a different sub-colony after failure. We add here that females and males exhibit quite similar levels of unconditional fidelity both toward their nest and toward their sub-colony.

While in other studies, both sexes exhibit WSLS behavior, some studies also demonstrate sexual differences in this behavior – in the Prairie Warbler (Nolan, 1978), in the Red-winged Blackbird (Beletsky and Orians, 1991) or in the European Sparrowhawk (Newton, 1993). Nevertheless, in these studies it is the female that usually displays the WSLS strategy.

Nesting failure in the Lesser Kestrel can result from various factors, including unfavorable microclimatic conditions (Bobek et al., 2018), nest predation, chick starvation, unfit or unexperienced parents, random effects, etc. Indeed, Serrano et al. (2001) indicate nest predation as one of the factors affecting colony dispersal by Lesser Kestrels in Spain. Nesting failure as a result of less fit parents, together with WSLS behavior, contribute to a fitness-associated dispersal (FAD), which in turn can have some evolutionary implications, such as accelerating the evolution of complex traits (Hadany et al., 2004).

A possible explanation to the sexual difference in WSLS behavior in our study can be attributed to the fact that individuals of each sub-colony in Jerusalem hunt together, each sub-colony in its distinct hunting areas. Hence, changing the hunting area entails moving to a different sub-colony. Calabuig et al. (2008) suggested that breeding dispersal in the Lesser Kestrel might result in part from a negative perception of the quality of the colony of origin affected by a bad breeding experience in the previous season. In line with this suggestion, those nesting failures that

result from poor nutrition may evoke a change of hunting area, and this can be achieved by moving to another sub-colony. In the Lesser Kestrel, the male is the main food provider (Gal, 2006). Thus, males may be more sensitive to such a possibility, and will more readily exert a WSL strategy towards the sub-colony.

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