



Breeding performance and nest-site selection of Woodchat Shrikes *Lanius senator* near the southern edge of their breeding distribution

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Received: 1 December 2023 / Revised: 18 January 2024 / Accepted: 6 February 2024
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Abstract

Numerous Woodchat Shrike (*Lanius senator*) populations, and Laniidae in general, are globally declining. A deeper understanding of their breeding ecology, including their nest-site selection and breeding performance, from hatching success to post-fledging survival, could contribute to their conservation. We studied breeding Woodchat Shrikes near the southern edge of their breeding range in Northern Israel, monitoring breeding pairs throughout the breeding season from March to July 2023 in three study areas at the slopes of the Golan Heights in a semi-open shrubland. We collected data on birds' nesting success, including hatching and fledging success, as well as on breeding pairs' productivity and post-fledging survival of Woodchat Shrikes. Furthermore, we gathered information on nest-site characteristics. In this part of their range, Woodchat Shrikes breed in relatively high densities, opportunistically selecting nest-sites within the area. Most pairs had at least two brood attempts and up to four were recorded. On average breeding pairs laid 4.63 eggs per brood, with a decreasing brood size later in the season. Breeding performance was not related to the nest-site characteristics with the exception of nest height above the ground, which had a positive influence on nesting success. The breeding performance of Woodchat Shrikes was relatively low compared to other studies, particularly when considering fledging success. Nest predation was likely a predominant cause for nest failures here; however, breeding pairs were able to substantially increase their breeding success with replacement broods. Compared to the low nesting success, the post-fledging survival was relatively high, indicating much higher predation pressure on nests compared to fledglings.

Keywords Breeding ecology · Nest-site characteristics · Post-fledging survival · Nesting success · Replacement broods

Zusammenfassung

Bruterfolg und Nistplatzwahl des Rotkopfwürgers *Lanius senator* am Südrand seiner Brutverbreitung

Viele Populationen des Rotkopfwürgers (*Lanius senator*) und der Laniidae generell sind weltweit rückläufig. Zu ihrer Erhaltung könnte beitragen, ihre Brutökologie, einschließlich der Wahl des Nistplatzes und des Bruterfolgs vom Schlüpfen bis zum Überleben nach dem Ausfliegen, zu verstehen. Wir untersuchten brütende Rotkopfwürger nahe dem südlichen Rand ihres Brutgebietes in Nordisrael und beobachteten die Brutpaare während der gesamten Brutsaison von März bis Juli 2023 in drei Untersuchungsgebieten in einem halboffenen Buschland an den Hängen der Golanhöhen. Wir sammelten Daten zum Bruterfolg der Vögel, einschließlich des Schlüpfens und Ausfliegens, zur Produktivität der Brutpaare, zum Überleben der Rotkopfwürger nach dem Ausfliegen und außerdem noch zu speziellen Merkmalen der Nistplätze. In diesem Teil ihres Verbreitungsgebiets brüten die Rotkopfwürger relativ nah beieinander, wobei sie ihre Nistplätze in dem Areal ganz willkürlich auswählen. Die meisten Paare hatten mindestens zwei Brutversuche, aber es konnten bis zu vier festgestellt werden. Im Schnitt legten die Brutpaare pro Brut 4,63 Eier, wobei deren Anzahl im Verlauf der Saison abnahm. Der Bruterfolg stand in keinem Zusammenhang mit irgendwelchen Merkmalen des Nistplatzes, mit Ausnahme der Nesthöhe über dem Boden, die

Communicated by F. Bairlein.

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sich positiv auf den Bruterfolg auswirkte. Im Vergleich mit anderen Untersuchungen war der Bruterfolg der Rotkopfwürger relativ gering, vor allem in Hinblick auf die Anzahl der flügge werdenden Jungvögel. Nesträuber waren hier wahrscheinlich die Hauptursache für die Verluste bei den Bruten; aber die Brutpaare konnten ihren Bruterfolg durch Zweitbruten erheblich steigern. Im Vergleich zum geringen Bruterfolg war die Überlebensrate nach dem Ausfliegen relativ hoch, was auf einen viel höheren Beutedruck auf die Nester als auf die Jungvögel hinweist.

Introduction

Declines in bird populations across Europe are largely driven by agricultural intensification and land-use changes since the twentieth century, causing negative population trends especially in birds adapted to open landscapes (Bowler et al. 2021; Rigal et al. 2023). However, spatiotemporal dynamics in bird population differ across Europe (Tryjanowski et al. 2011). These dynamics also depend on birds' migration strategies; long-distance migrants have exhibited greater decline (Bowler et al. 2021) and generally have lower seasonal breeding performance due to the shorter time for breeding in their annual cycle (Smith and Moore 2005). To implement effective conservation measures averting further population declines, it is crucial to gain knowledge on species' breeding ecology and environmental requirements (Tryjanowski et al. 2011). In addition to nesting success (nests producing at least one fledgling) and breeding success (pairs producing at least one fledgling), information on breeding performance should also include fledglings' survival during the period after young birds leave the nest and until they disperse or migrate, referred to as post-fledging survival (Anders and Marshall 2005; Cox et al. 2014). During this post-fledging period, many young rely on parental care, especially for species with short nesting periods (Grübler and Naef-Daenzer 2010). Even though this period is particularly relevant in species fitness, it is under-studied in most passerines and thus studies quantifying the survival during this period are crucial (Anders and Marshall 2005; Cox et al. 2014).

As many other members of the Laniidae family, Woodchat Shrikes (*Lanius senator*) are adapted to open landscapes and preferably breed in semi-open, dry grassland habitats with scattered shrubs, but they are also found in agricultural fields with sufficient shrub-like cover (Isenmann and Fradet 1998). Furthermore, most members of the Laniidae family worldwide are declining (Yosef 1994; Lefranc 2022), and so are many European breeding populations of the Woodchat Shrike (Yosef 2008). Reduction and degradation of the Shrikes' breeding habitat and increased mortality in the breeding grounds and along their migration routes have caused population declines, especially in Northwest Europe (Yosef and Tryjanowski 2000; Yosef 2008; Lefranc 2022). Woodchat Shrikes prey almost exclusively on large invertebrates, requiring prey-rich habitats with certain

habitat structures for their "sit-and-wait" hunting strategy, but most suitable habitat types are shrinking throughout Europe (Cramp et al. 1993; Yosef 2008). Although their northern breeding distribution range is contracting, Woodchat Shrikes are still common in most of their southern breeding areas (Yosef 2008). Thus, despite their decline, they are not considered to be globally threatened (BirdLife International 2023).

We studied Woodchat Shrikes (subspecies: *L. s. niloticus*) in Northern Israel, along the slopes of the Golan Heights. This is one of the southernmost breeding locations of this species. Consequently, *L. s. niloticus* have a shorter migration route to their Northeast African wintering grounds, resulting in a longer breeding season compared to the European subspecies (Cramp et al. 1993). We studied the breeding performance of Woodchat Shrikes during different stages of their breeding season and estimated the survival of their eggs, nestlings, and fledglings. This study also investigated the nest-site selection to understand how it affected the birds' breeding performance. Here, we investigated: (1) nest-site selection and breeding densities of Woodchat Shrikes; (2) if breeding performance was affected by nest-site selection; and (3) post-fledging survival rate and breeding productivity. This study enhances our understanding of Woodchat Shrike breeding ecology, allowing us to determine which nest-site characteristics contribute to successful reproduction, in a population near the southern edge of the species' breeding distribution range.

Materials and methods

Data collection

During the breeding season from March to July 2023, we monitored Woodchat Shrikes in three study areas, of 22–29 ha, that consist of semi-open shrubland with extensive grazing pressure: Ein Tina (33°04'56.0"N, 35°38'45.1"E), Nahal Neshef (33°05'38.0"N, 35°38'46.5"E), and Nahal Orvim (33°09'02.5"N, 35°39'30.6"E). Each study area was visited weekly searching for nests to record the number of eggs or nestlings as well as to collect information on nest-site characteristics, i.e., nest height above the ground, nest concealment, and nest-supporting shrub species. The nest concealment categories (see Fig. 1c, d, e) were defined evaluating

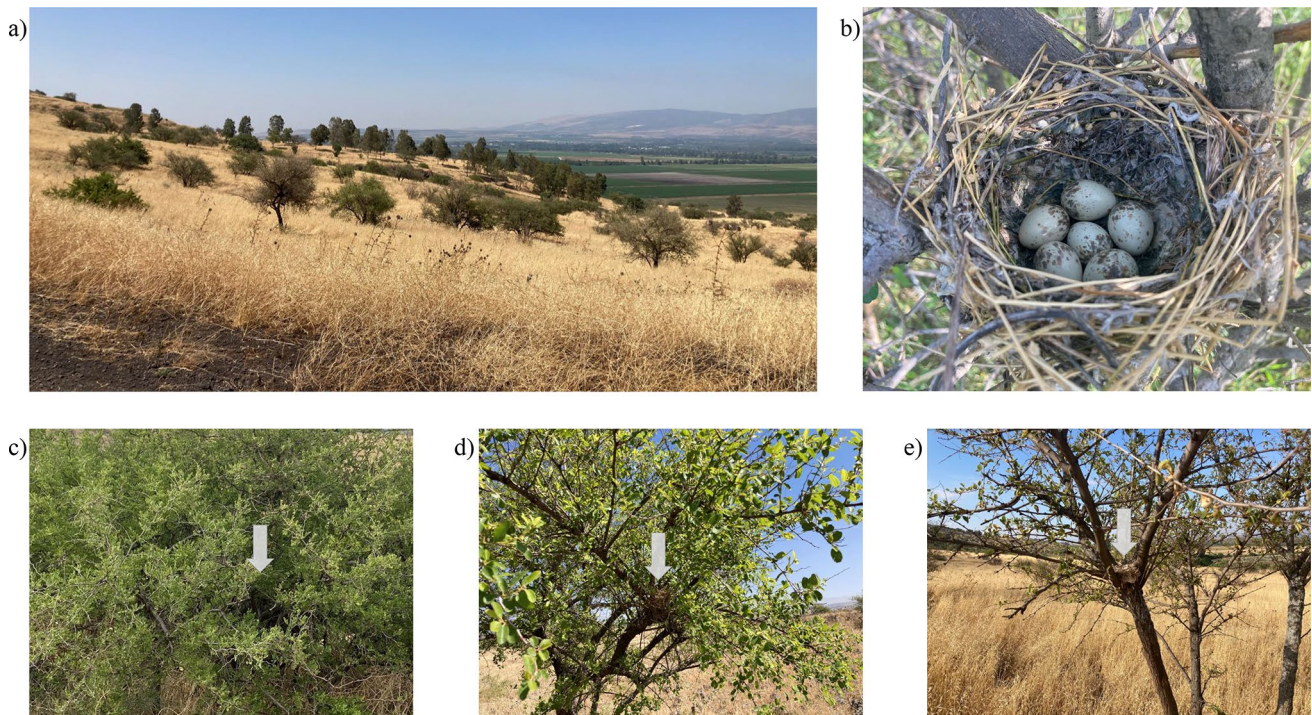


Fig. 1 Images of **a** the predominant semi-open shrubland habitat at the study areas and **b a** Woodchat Shrike (*Lanius senator*) nest. Three nest concealment categories were defined: **c** densely concealed nests,

which cannot be easily seen, **d** intermediately concealed nests, which are only partially visible, and **e** open nests, that are completely visible. The light grey arrow indicates the nest location within the shrub

the nests' visibility from two points, at a 90-degree angle to one another, when standing two meters in front of the nest-supporting shrub. By revisiting the nest-sites weekly, we monitored the Shrikes' breeding performance. To minimize nest failures due to human disturbance, specific nests that contained eggs were only controlled again after two weeks (Shirihai 1996; Tryjanowski and Kuźniak 1999). From approximately 8-days of age, nestlings were ringed with unique combinations of coded metal rings and uncoded colour rings. This enabled individual identification of the young during the regular (i.e., at least twice a week) resighting visits of pairs with fledglings during the post-fledging period, using binoculars and a spotting scope. Meteorological data were collected from the Israeli Meteorological Service's weather station of in Kfar Blum, about eight km northwest of the study areas (Israel Meteorological Service Meteorological Database 2023).

Data analysis

We calculated the weekly breeding pair density per ha for each study area from the number of active breeding pairs (i.e., incubating or with nestlings), based on field observations and estimated egg-laying dates. For nests found with only the first egg laid or with nestlings ($n=29$), we estimated

the one- to two-day precise egg-laying date retrospectively, after identifying nestling ages in days post-hatching, following the description for aging Red-backed Shrike (*Lanius collurio*) nestlings by Van den Burg et al. (2011). For the remaining nests ($n=32$), we estimated the two- to 12-days precise egg-laying date from the number of eggs in combination with field observations or the age of the fledglings, identified from morphological characteristics. To calculate the egg-laying date, we used the mean incubation (15 days) and nestling periods (16 days) described in other studies of Woodchat Shrikes (Ullrich 1971; Shirihai 1996; Bechet et al. 1998; Isenmann and Fradet 1998; Nikolov 2005; Yosef 2008). Using recent aerial images (0.6 m resolution) in ArcGIS 10.6.1 (Esri Inc. 2023), we performed spatial analyses calculating additional nest-site characteristics. We identified the distance to the nearest neighbouring active nest, the position of the nest-supporting shrub in relation to other shrubs, the distance between nests used for different brood attempts by the same pair and the number of shrubs in the territory. We used a 1.5 ha large buffer area around each nest as territory, since this territory size was described in other studies (Yosef 2008) and fits to the density and mean distance between nests in the present study. To calculate the mean clutch size, we included nests with at least two eggs, because two to seven eggs were found in the nests

with information on complete clutch, as confirmed from a second nest visit (see SI1). We tested if the clutch size varied in relation to the egg-laying date, using a Spearman's Rank Correlation, and between the number of brood attempts, using a Kruskal–Wallis test and Dunn's post-hoc test. We tested the re-nesting distance in relation to the distance to the nearest neighbouring active nests using a Spearman's Rank Correlation. Additionally, we tested if the probability for a replacement brood depends on the egg-laying date of the failed brood attempt using a binomial Generalized Linear Model (GLM). Brood attempts were identified based on observed behaviours and movements of the breeding pairs during the weekly site visits. Since nearly half of the breeding pairs had at least one colour-ringed adult (i.e., 15 out of 31 pairs), we were able to follow relocation movements during replacement broods.

We calculated various variables of the Woodchat Shrikes' breeding performance: a brood attempt was defined if at least one egg was laid. For these nests we calculated the hatching success (percentage of eggs that hatched from laid eggs), fledging success (percentage of fledged young from hatched nestlings) and nesting success (percentage of nests with at least one fledgling). For breeding pairs, we calculated the breeding success (percentage of pairs with at least one fledgling) and productivity (number of fledglings, both for all and only for successful pairs).

To test whether nest-site selection influenced nesting success, we ran a binomial Generalized Linear Mixed Model (GLMM) with the breeding pair as random factor and different variables related to the nest-site characteristics: study area (Ein Tina, Nahal Neshef or Nahal Orvim), nest concealment (dense, intermediate or open), nest height above the ground, shrub species (*Ziziphus spina-christi*, *Ziziphus lotus*, or *Pistacia atlantica*), shrub position (solitary or in a shrub group), weekly breeding pair density while the nest was active, distance to nearest neighbouring nest, and number of shrubs in the pair's territory ($n = 62$ nests). The different models were ranked according to their AIC value, and the best fitted model with a subset of variables (i.e., nest height, nest concealment, and shrub species, see SI6) was selected as the final model. Furthermore, we performed binomial GLMM, with the breeding pair as random factor, to test for a possible correlation between nesting success and clutch size ($n = 52$), estimated egg-laying date ($n = 61$), and different brood attempts ($n = 60$), respectively. We used binomial and poisson GLMMs, with the breeding pair as random factor, to test how breeding success and productivity of breeding pairs ($n = 31$), respectively, varied with the different nest-site selection factors: study area, mean nest height above the ground, mean weekly breeding pair density, mean distances to nearest neighbour, and number of shrubs in the territory.

To study post-fledging survival, we calculated the young survival over the study period (8–49 days after hatching) as a product of the daily apparent survival rate (i.e., probability that an individual is alive) for each day. We estimated the daily apparent survival rate and the probability to observe an individual for each day running a “young survival for marked adults” model, an extension to the Cormack-Jolly-Seber model with resighting data of the colour-ringed young of each breeding pair (Lukacs and Dreitz 2008), in the program MARK 9.0 (White 2021). To test if the daily apparent survival was related to their age, we ran a Spearman's Rank Correlation.

All statistical analyses were performed in RStudio using R version 4.3.1 (R Core Team 2023). All tests were two-tailed with α of 0.05.

Results

Nest-site selection, clutch size, and breeding phenology

Woodchat Shrikes breed in densities with an average of 0.32 active breeding pairs per ha ($SD = 0.10$) and with 130.65 m ($SD = 49.84$) between active nests. The number of shrubs in their territories varied substantially, ranging from 2 to 79 shrubs (mean = 39.16; $SD = 18.71$). The birds built their nests mostly in *Ziziphus spina-christi* shrubs (87.1%). The majority (54.8%) of nest-supporting shrubs stood solitarily, and the nest was often openly exposed (43.6%); only 17.7% of the nests were hidden in dense shrubs. The nests were 1.17–42 m above the ground level, with a mean height of 1.93 m ($SD = 0.65$).

The mean clutch size was 4.63 ($SD = 1.25$), ranging from 2 to 7 eggs (Fig. 2). Many (77.8%) breeding pairs had at least one additional brood attempt, but up to four brood attempts were recorded. The clutch size was significantly lower in the third compared to the first ($p < 0.001$, $Z = 4.01$) and second broods ($p < 0.05$, $Z = 2.89$, SI2) and decreased significantly with later egg-laying date ($p < 0.01$, $r_s = -0.59$, SI3). On average, the re-nesting distance between brood attempts was 69.7 m ($SD = 45.18$, range: 10.7 to 235.7 m, $n = 32$). The re-nesting distance was not significantly correlated with the distance to the nearest neighbouring breeding pair (SI4). More than half of the failed nests (65.1%) had a replacement brood. The probability for a replacement brood was significantly lower ($p < 0.01$, $b = -0.13$, $n = 43$, SI5) with later egg-laying dates and brood attempts that failed after the 6th of June had no replacement broods.

Woodchat Shrikes started to breed, i.e., laid eggs of their first brood attempt, on average on the 17th of April

Fig. 2 Histogram of the clutch size from nests of Woodchat Shrikes (*Lanius senator*) with at least two eggs ($n=52$ nests)

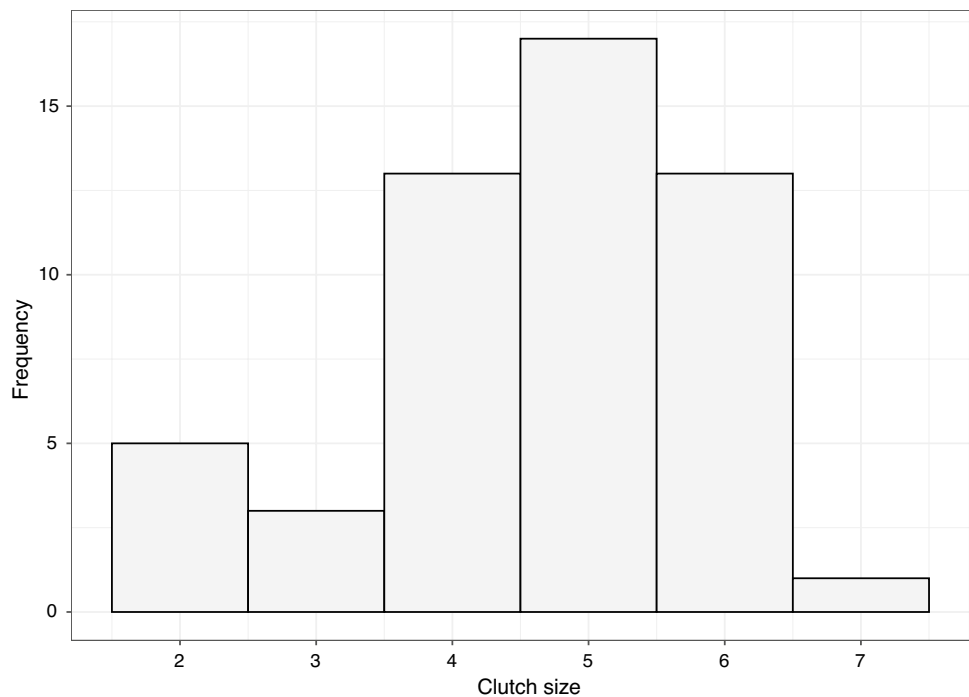
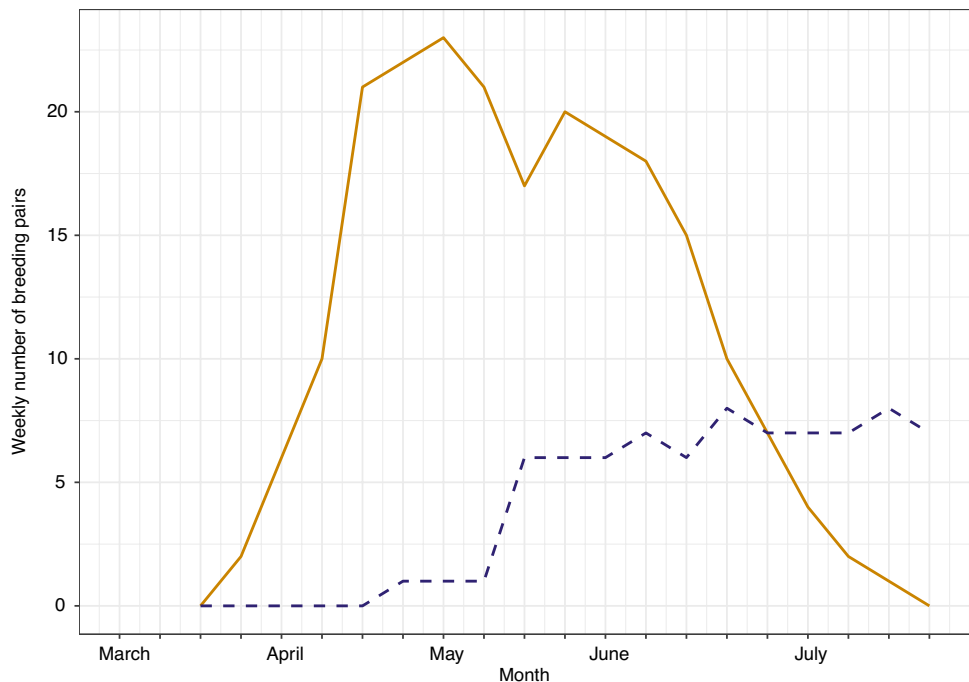


Fig. 3 Breeding phenology of Woodchat Shrikes (*Lanius senator*). Weekly number of breeding pairs with eggs or nestlings (orange, solid line) and pairs with fledglings (blue, dashed line) for the breeding season from the end of March to the end of July 2023



(SD=8.22, $n=25$), but this varied between breeding pairs, with a total range of 36 days between the earliest pair (end of March) and the last (beginning of May). The breeding phenology (Fig. 3) had two peaks, of pairs either incubating or with nestlings, in the beginning and at the end of May. From the end of April, the first breeding pairs were already observed with their fledglings.

Breeding success, productivity, and post-fledging survival

Of the brood attempts with at least one laid egg, 55.4% hatched successfully and 29.8% of the hatched young also survived until fledging. Consequently, the overall nesting success was 21.9%. However, due to the replacement

broods of breeding pairs with failed attempts, the breeding success was increased to 39.3%. Most of the failed nests (60%) were found empty but undestroyed, as after predation due to avian or reptile nest predators (Yosef 2000). None had dead nestlings inside, as it is the case after nest failure due to bad weather events (Mirkov 1984). Days with over five mm rainfall recorded after the earliest egg-laying date were rare, with a single event on the 29th of April (7.9 mm) (Israel Meteorological Service Meteorological Database 2023). On average, the breeding pairs produced 1.19 fledglings when considering all pairs, and 3.08 fledglings when considering only the successful pairs (Table 1).

The GLMM that included the variable nest height (together with nest concealment and shrub species) was the best fitted model according to its AIC (61.00) with a weight of 0.089. The second-best model had an AIC of 61.36 (SI6). Nesting success was significantly and positively ($p < 0.05$, $b = 1.70$, SI7) related to the nest height. All other variables related to the nest-site selection were not significant in models of nesting success, breeding success, or productivity (SI7, SI11–SI12). The clutch size, egg-laying date, and different brood attempts also did not affect nesting success (SI8–SI10).

Using field observations of colour-ringed young, we found that fledglings dispersed from their natal nest-site 16–41 days after fledging. Until then, they remained together in family groups under parental care. Over this period, young had a mean survival rate of 0.739 (SD = 0.33). The daily apparent survival of the young increased significantly ($p < 0.001$, $r_s = 1$, Fig. 4, SI13) with their age.

Discussion

Nest-site selection and breeding ecology

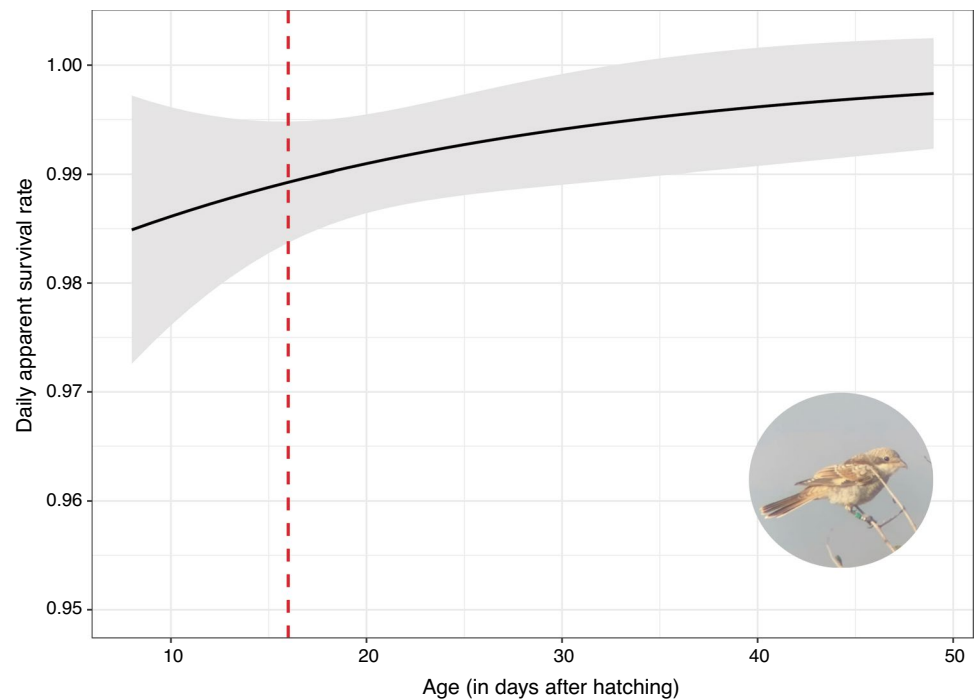
Woodchat Shrikes at our study area breed in their generally preferred habitat type, a semi-open shrubland (Isenmann and Fradet 1998; Yosef 2008). It provides all required habitat structures (Yosef 2008), and the birds show some flexibility in relation to shrub density preference, a habitat attribute which varied substantially between territories. As also found in other studies, Woodchat Shrikes are largely opportunistic in their choice of nest support, selecting the most common shrub species (Isenmann and Fradet 1998), which, in the present study, was the *Ziziphus spina-christi*, a thorny but loosely vegetated shrub species. Thus, most nests in our study area were poorly concealed. Nest height varies widely within and between studies (Cramp et al. 1993). Compared to European study areas (Cramp et al. 1993), nests in the present study were rather low (mean height of 1.93 m above the ground), similar to those reported from other Mediterranean populations (Yosef 2008). Southern populations, like in the present study, breed in more clustered structures, with smaller territory sizes, than in Central Europe (Yosef 2008). The mean distance of 130.65 m between active nests in this study, also indicates a small territory size like the 1.5 ha described for Woodchat Shrikes in Georgia (Yosef 2008). The relatively high breeding density of 0.32 pairs per ha is slightly higher than 0.18/ha in Algeria (Moali et al. 1997) and similar to 0.3/ha in Morocco (Brosset 1961), but not as high as the exceptionally dense breeding populations in Spain with 1.03 pairs per ha (Rehsteiner 2012) or 1.65/ha in Bulgaria (Karaivanov 2005). Nevertheless, to calculate the density, we only included breeding pairs incubating or with nestlings, while other studies used data from all the present

Table 1 Hatching, fledging, nesting, and breeding success and productivity per breeding pair (BP) for Woodchat Shrikes (*Lanius senator*) in the present study compared with other studies. The studies are

in order from their approximate latitude of their study area with the southernmost in the end of the table. If available, the sample size is mentioned for each calculated variable

Country	Hatching success (%)	Fledging success (%)	Nesting success (%)	Breeding success of all BP (%)	Productivity of all BP	Productivity of successful BP	Reference
Slovakia	58.1 ($n = 75$)	49.5 ($n = 75$)			2.44		(Hudec and Černý 1983)
Germany	68.9 ($n = 112$)	42.0 ($n = 112$)			2.3	3.43	(Ullrich 1971)
Germany						4.55 ($n = 180$)	(Ullrich 1987)
France			36.9 ($n = 164$)				(Isenmann and Fradet 1998)
Bulgaria	53.4 ($n = 30$)	41.2 ($n = 30$)	24.6 ($n = 30$)				(Nikolov 2005)
Israel	55.4 ($n = 22$ nests)	29.8 ($n = 21$ nests)	21.9 ($n = 64$ nests)	39.3 ($n = 31$)	1.19 (SD = 1.66; $n = 31$)	3.08 (SD = 1.08; $n = 11$)	Present study

Fig. 4 Estimate of the daily apparent survival rate (black line) with the standard error (grey area) of 8- to 49-day-old Woodchat Shrikes (*Lanius senator*) increased significantly ($p > 0.001$, $r_s = 1$, SI13) with age (i.e., days after hatching). The data is from seven breeding pairs with colour-ringed young ($n = 27$ young). The vertical, red, dashed line indicates 16-days of age, post-hatching, when nestlings usually fledge (Ullrich 1971; Shirihai 1996; Bechet et al. 1998; Isenmann and Fradet 1998; Nikolov 2005; Yosef 2008)



adults with a territory. Using that classification would also include family groups with fledglings (see Fig. 3), resulting in a higher density of up to 0.41 breeding pairs per ha.

The mean clutch size of 4.63 eggs was slightly lower than those described in other studies, which only included clutches with at least three eggs (Ullrich 1971; Bechet et al. 1998; Isenmann and Fradet 1998; Nikolov 2005; Yosef 2008). However, the complete clutches found in the present study ranged from two to seven eggs (SI1), indicating a smaller minimum clutch size. Woodchat Shrikes in the present study had a decreasing clutch size both with each replacement clutch and with the progression of the breeding season, a pattern commonly observed in many Shrike species (Ullrich 1971; Isenmann and Fradet 1998; Kristin et al. 2000; Antczak et al. 2009). Most breeding pairs had more than one brood attempt, which is usual in Middle Eastern and North African breeding population (Cramp et al. 1993; Yosef 2008). Interestingly, one colour-ringed female laid eggs in four brood attempts, an exceptionally high number that was not described before for Woodchat Shrikes. The Shrikes had a replacement brood after more than half of the failed brood attempts recorded, even more often than the Woodchat Shrikes in Mediterranean France (Isenmann and Fradet 1998). Replacement broods are costly, and for Red-backed Shrikes, the size and probability of a replacement clutch depends on the stage of the failed brood (Antczak et al. 2009). The present study did not have sufficiently large sample size on the stage of the nest failure to explicitly test this pattern. Nevertheless, this information was likely important in the decision-making process of the breeding

pairs, as the probability for a replacement brood decreased significantly over the breeding season and failed broods with eggs laid after the 6th of June were not replaced anymore. The majority of Woodchat Shrikes in our study re-nested within the 1.5 ha territory around their previous nest-site, as was also observed for Red-backed Shrikes (Antczak et al. 2009). Some Woodchat Shrikes, however, were found to re-nest outside their previous territory, up to 235.7 m away, indicating some spatial flexibility. However, the re-nesting distance seems to be independent of the distance to the pair's nearest neighbour.

In line with the description in the literature (Shirihai 1996), our field observations suggest that the first birds of the *L. s. niloticus* subspecies arrive from migration to their breeding grounds as early as March. Their egg-laying largely began in April, slightly later and more variably than described previously for breeding populations in Israel, yet it was still substantially earlier than in Central Europe (Yosef 2008). In Central Europe, the Woodchat Shrikes must start their nest building considerably faster after arriving at the breeding grounds (Ullrich 1971), indicating important time-constraints during their shorter breeding season due to longer migration distances compared to the *L. s. niloticus* subspecies (Cramp et al. 1993). This might also be supported by their summer moult pattern, where the nominate subspecies does not replace any flight feathers (Svensson 1992), while adult *L. s. niloticus* Woodchat Shrikes only retain a few secondaries from their extensive split moult (Kiat and Izhaki 2022).

The importance of nest-site selection for breeding success

Woodchat Shrikes with nests higher above the ground had a significantly higher nesting success in this study, a pattern previously observed across several passerine species (Li and Martin 1991), including Loggerhead Shrikes (*Lanius ludovicianus*) (Nur et al. 2004). Higher nests might be safer from ground predators, like some mammals and reptiles, since Great Grey Shrikes (*Lanius excubitor*) increased their nest height after human disturbance (Antczak et al. 2005). However, some studies on Woodchat, Red-backed- and Great Grey Shrikes found little or no evidence for the importance of nest height on nesting success (Yosef 1992; Isenmann and Fradet 1998; Tryjanowski et al. 2000). In the present study, the GLMM including the variable nest height had relatively low support, with a weight of only 0.089, and several other models were within ΔAIC less than two (SI_6), the widely accepted “substantial level of empirical support” threshold (Burnham and Anderson 2002).

No other nest-site characteristics showed importance for Woodchat Shrike breeding performance, i.e., nesting success, breeding success or productivity, in support of other studies (Isenmann and Fradet 1998). Similarly, for a variety of passerines, including Shrikes, there was no effect of nest concealment on breeding success (Isenmann and Fradet 1998; Campos et al. 2011; Golawski et al. 2023). In studies that also included thornless deciduous shrubs, the Iberian Grey Shrike (*Lanius meridionalis*) and Red-backed Shrike both had higher success in the thorny than in thornless shrubs (Tryjanowski et al. 2000; Campos et al. 2011). In our study, all three nests in the thornless *Pistacia atlantica* were predated, but the low sample size did not allow for a statistical comparison to the 59 nests found in thorny shrubs. The properties of thorny shrubs as nest sites seem to increase the effectiveness of nest defence in Red-backed Shrikes, especially during the early nestling stage (Tryjanowski et al. 2000; Golawski and Mitrus 2008). However, higher visibility from the nest might be beneficial for adults who can start warning others and defending their nest earlier than from highly concealed nests (Golawski et al. 2023). While studies on the closely related Red-backed Shrike show the importance of a parent's aggressiveness for the breeding success (Golawski and Mitrus 2008), corresponding studies in Woodchat Shrikes are lacking. Interestingly, aggressive behaviour against potential avian nest predators, i.e., Hooded Crows (*Corvus cornix*) and Eurasian Jays (*Garrulus glandarius*), were frequently observed at the study areas (personal observations), stressing the need for further studies on the importance of aggressiveness for nesting success of Woodchat Shrikes. In previous studies, general breeding habitat type affected breeding performance in Red-backed Shrikes (Bloche et al. 2023), possibly because

predation danger is related to the breeding and surrounding habitat types (Matyjasiak 1995; Söderström et al. 1998). In our study the habitat type was essentially the same in all the study areas, but in further studies, breeding pairs from other habitat types should be compared, e.g., Woodchat Shrikes breeding higher up in the Golan Heights or even at the nearby Mt. Hermon in mountainous habitats between 1000 and 1600 m above sea level (Shirihai 1996).

Woodchat Shrikes in the present study had a relatively low nesting success compared to other studies (Bechet et al. 1998; Isenmann and Fradet 1998; Nikolov 2005). Specifically, fledging success was severely lower than in other studies, while the hatching success seems to be similar (Ullrich 1971; Hudec and Černý 1983; Nikolov 2005). This difference between hatching and fledging success indicates that most nest failures were during the nestling stage. During this period, the frequent nest visits by feeding adults might make the nests more conspicuous to predators (Martin et al. 2000). Golawski et al. (2023) also found lower survival during the nestling stage, while Nikolov (2005) found that most nesting attempts of Woodchat Shrikes failed before hatching.

The results of our one-year study should be treated with caution, as Shrike breeding populations can fluctuate strongly between years (Ullrich 1971, 1987; Bloche et al. 2023; Golawski et al. 2023). Nevertheless, Bechet et al. (1998) did not find fluctuation of the predation rate on Woodchat Shrikes nests. The Woodchat Shrikes in our study were able to increase the originally low nesting success with replacement broods to a much higher success rate of 39.3% for the pairs' breeding success. This stresses the importance of replacement broods for the long-term maintenance of Shrike populations. To have the chance for re-nesting after a failed brood attempt, Red-backed Shrikes evolved to start nesting as early as possible (Antczak et al. 2009). While the European populations of Woodchat Shrikes only arrive at the breeding grounds in mid-May (Cramp et al. 1993), the *L. s. niloticus* subspecies might already start its second brood in May. This is a critical advantage of short-distance migration, also demonstrated through generally higher annual fecundity (Bruderer and Salewski 2009) and seasonal breeding performance (Smith and Moore 2005) of short-distance migrants, compared to long-distance migrants.

Nest predation likely was the predominant cause for nest failures in this study, as it was for Woodchat Shrikes in Bulgaria (Nikolov 2005) and Mediterranean France (Bechet et al. 1998). This was also documented for other Shrike species, including Lesser Grey Shrikes (*Lanius minor*) in Slovakia (Kristin et al. 2000) and Great Grey Shrikes in Israel (Yosef 1992, 1993). While inclement weather, i.e., cold and rainy periods, is a common cause for nest failures in Central Europe (Ullrich 1971), it was probably not as relevant in our study area. The single rain event documented during this study was within the period

in which only six out of 38 nest failures occurred, and no nest was found with dead nestlings, as is typically the case after inclement weather (Mirkov 1984). Other studies of Mediterranean breeding populations mention several potential nest predators of Woodchat Shrikes (Bechet et al. 1998). Avian nest predators were commonly observed at our study area (personal observations). Moreover, several reptiles, like snakes and the European Glass Lizard (*Ophisaurus apodus*), as well as mammals, are potential nest predators in the Mediterranean shrubland (Ben-David et al. 2019). Most failed nests here were found empty and undestroyed, which, according to Yosef (2000), indicates predation by avian or reptile nest predators and not mammals. The significant effect of nest height on nesting success might indicate the importance of ground predators, i.e., reptiles. However, further studies are needed to identify and quantify the specific nest predators of Woodchat Shrikes in Israel, since predation seems to greatly decrease their nesting success.

Breeding productivity and post-fledging survival

The Woodchat Shrikes had relatively low breeding productivity due to the low nesting success. While the productivity of successful pairs was only slightly lower than in other studies, the productivity of all breeding pairs was severely below what was found in comparable studies (Ullrich 1971; Hudec and Černý 1983); however, the survival rate of the young after fledging was substantially higher. The post-fledging survival rate of 0.739 for young Woodchat Shrikes is similar to results for Red-backed Shrikes (0.73) (Bloche et al. 2023) and Loggerhead Shrikes (0.76) (Imlay et al. 2010). The daily survival rate of young Woodchat Shrikes increased over the post-fledging period (Fig. 4) along with increasing independence from parental care (Nikolov and Hristova 2007; Bloche et al. 2023). This pattern is commonly observed across passerines, including Shrikes (Yackel Adams et al. 2001; Cox et al. 2014; Bloche et al. 2023). Even though parental care during this period is crucial for the survival of the young (Nikolov and Hristova 2007), we found large variation in the length of the period when fledglings stay in family groups at their natal nest-site until dispersal. While some only stayed for just over two weeks after fledging, as described by Shirihai et al. (1996), fledglings in other breeding pairs stayed for up to six weeks, as described in other studies (Nikolov and Hristova 2007; Yosef 2008). Further studies on the behaviour, movements and dispersal of young Woodchat Shrikes are needed to better understand the causes and consequences of this variation.

Conclusion

Aside from the nest height above ground, no other nest-site characteristics were related to Woodchat Shrikes breeding performance in this study. Similar to comparable studies, nesting success substantially decreased, as a result of predation, before young fledged (Isenmann and Fradet 1998). This study stresses the importance of replacement broods for the overall breeding success in Shrikes (Antczak et al. 2009) and the advantages of having fewer breeding time-constraints in short-distance migrants (Smith and Moore 2005). When developing conservation measures in different regions, the importance of replacement broods and differences in breeding time-constraints between different populations needs to be considered. Furthermore, the high breeding densities at the study area indicate the importance of semi-natural habitat types, i.e., semi-open shrubland with extensive grazing pressure. Since nest-site selection might be less important for breeding performance than the local abundance of predators (Golawski et al. 2023), it is crucial to identify specific nest predators of Woodchat Shrikes. Additionally, we highlight important knowledge gaps regarding the length of the post-fledging period under parental care as well as post-fledging dispersal behaviour and movement. It is crucial to close these knowledge gaps to create species-specific conservation measures for Woodchat Shrikes in Israel, near the southern edge of their breeding distribution.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10336-024-02157-0>.

Acknowledgements We are grateful to Angelia Ellvin and Daniela Zinßmeister for their assistance in preparing and conducting the fieldwork and to the Israeli Meteorological Service for providing the meteorological data.

Author contributions Both authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Daniel A.F. Bloche. The first draft of the manuscript was written by Daniel A.F. Bloche and Nir Sapir commented on previous versions of the manuscript. Both authors read and approved the final manuscript. No funding was received for conducting this study. This is an observational study without invasive procedures. A permit from the Israel Nature and Parks Authority (No. 2023–43275) was granted for undertaking this study.

Funding Open access funding provided by University of Haifa.

Data availability The main data from the figures and results are public available on figshare.com via the following link: https://figshare.com/projects/Breeding_performance_and_nestsite_selection_of_Woodchat_Shrikes_Lanius_senator_near_the_southern_edge_of_their_breeding_distribution/198508.

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