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ORIGINAL ARTICLE

Egyptian Nightjars are residents in the Dead Sea region, showing a high year-round roost fidelity

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Abstract
We investigated the spatial behavior of a recently discovered breeding population of Egyptian Nightjars (*Caprimulgus aegyptius*) near the Dead Sea. While there is a prevalent migratory tendency in other populations of this species, it is unknown whether this recently discovered population is migratory or sedentary. To resolve this uncertainty, we examined their daily and annual movements by equipping five individuals (two adults, three juveniles) with GPS tags and retrieved data from the two adults (a female and a male). Sampling Nightjar's location twice a day (once during the nighttime and once during the daytime) over a period of eleven months, we found that they exhibited resident behavior. They remained in the same area for the entire tracking period, travelling as little as 15.1 km from the tagging location, and 2.4 ± 1.7 km (mean ± SD) daily. We also documented high roost fidelity, showing a tendency to return to the same day-roost site every day within a radius of 30 m, usually in a shady spot under a small bush, and a continuous use of the same site for up to five months, during both summer and winter. Our findings confirm that at least a part of the Egyptian Nightjar population in the Dead Sea region is resident, and highlight the ecological and conservation importance of their specific, and repeatedly used, daily roost sites and year-round activity areas.

Keywords Nightjars · Migration · Residency · Roost fidelity · GPS tracking · Movement ecology

Zusammenfassung
Pharaonennachtschwalben aus der Region des Toten Meeres zeigen ganzjährig eine ausgeprägte Schlafplatztreue.
Wir untersuchten das Standortverhalten einer erst kürzlich nahe dem Toten Meer entdeckten Brutpopulation von Pharaonenachtschwalben (*Caprimulgus aegyptius*). Während andere Populationen dieser Art gerne umherziehen, weiß

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man nicht, ob es sich bei dieser kürzlich entdeckten Population um eine wandernde oder eine ortstreue Population handelt. Zur Klärung dieser Frage untersuchten wir ihre täglichen und jährlichen Flugbewegungen, indem wir fünf Individuen (zwei erwachsene Tiere, drei Jungtiere) mit GPS-Transpondern ausstatteten und die Daten von den zwei erwachsenen Tieren (einem Weibchen und einem Männchen) abriefen. Wir erfassten die Standortdaten der Pharaonennachtschwalben elf Monate lang zweimal täglich (einmal nachts und einmal tagsüber) und stellten fest, dass sie sehr ortstreu waren. Sie hielten sich während der ganzen Untersuchungszeit in demselben Gebiet auf, entfernten sich nur 15,1 km vom Ort ihrer Markierung und legten pro Tag nur 2,4 ± 1,7 km (Mittelwert ± SD) zurück. Wir konnten ferner eine hohe Schlafplatztreue nachweisen, bzw. die Neigung, jeden Tag zum gleichen Schlafplatz im Umkreis von 30 m zurückzukehren, in der Regel ein schattiger Platz unter einem kleinen Busch, und diesen Ort über einen Zeitraum von bis zu fünf Monaten sommers wie winters regelmäßig aufzusuchen. Unsere Ergebnisse bestätigen, dass zumindest ein Teil der Population der Pharaonennachtschwalben im Gebiet des Toten Meeres standorttreu ist und unterstreichen die ökologische und naturschutzrelevante Bedeutung ihrer individuell und regelmäßig genutzten Tagesschlafplätze und der Areale, in denen sie aktiv ganzjährig unterwegs sind.

Introduction

Migration allows birds to cover long distances to find favorable habitats and environmental conditions. Residency may force them to cope with local conditions year round, but it avoids the adaptations and high costs induced by migration (Dingle and Drake 2007; Newton 2007; Lovette et al. 2016). Indeed, 81.5% of 9832 bird species with available data are residents (Rolland et al. 2014), remaining in the same area year-round, and relying on locally available resources to fulfil their biological and ecological needs, such as foraging, breeding, thermoregulation and predator avoidance. Desert ecosystems present unique challenges, characterized by extreme temperatures, high potential evapotranspiration indices, and limited resources. This often drives species to adopt nocturnal activity to avoid the intensive diurnal heat and sun radiation (Costa 1995), or in the case of regional nomadism to seek ephemeral beneficial conditions (Dean 2004). The effects of these extreme conditions on the natural history traits of desert species are most pronounced in resident species that need to deal with these challenging conditions year-round. However, nocturnal desert species are particularly understudied, primarily due to the difficulties associated with conducting studies in these environments, resulting in poor knowledge of their basic natural history, such as migration behavior or roosting behavior (Roll et al. 2017; Gaston 2019; Jung et al. 2021).

The nightjars family (*Caprimulgidae*) includes various nocturnal species, many of which live in arid areas and suffer from limited information regarding their natural history. Migratory behavior varies considerably between Nightjar species, and even among populations within a species. Some species like the European Nightjar (*Caprimulgus europaeus*) and the Common Nighthawk (*Chordeiles minor*) undertake long-distance intercontinental migration (Evens et al. 2017; Ng et al. 2018), while some other species, such as the Antillean Nighthawk (*Chordeiles gundlachii*), the Pennant-winged Nightjar (*Caprimulgus vexillarius*) and the Sykes's Nightjar (*Caprimulgus mahrattensis*) perform a short, intracontinental, or even partial migration (Cleere and Kirwan 2020; Perlut and Levesque 2020; Cleere et al. 2021). In contrast, species like the Star-spotted Nightjar (*Caprimulgus stellatus*) and the Choco Poorwill (*Nyctiphrynus rosenbergi*) are known to be residents, while others, such as the Prigogine's Nightjar (*Caprimulgus prigoginei*) are understudied (Byington 2020; Cleere 2020a; Cleere et al. 2020a). Within a season, nightjar species also tend to show high roost site fidelity. For example, the Eastern Whip-poor-will (*Antrostomus vociferus*) tend to return to the same roosting site at the wintering grounds, the Nubian Nightjar (*Caprimulgus nubicus*) was found to use the same roost site repeatedly, and the Common Nighthawk was documented using the same roost tree for several consecutive days (Holyoak 2001; Jetz et al. 2003; Fisher et al. 2004; Perlman 2007; Campbell and Smiles 2018; Tonra et al. 2019; Cleere 2021).

Our study species, the Egyptian Nightjar is a nocturnal mid-sized Nightjar species that inhabits arid and semi-arid regions in Africa and Asia. Like many other members of its family, it is a cryptic species, relying on its highly camouflaged plumage for protection and predator avoidance (Holyoak 2001; Wilson-Aggarwal et al. 2016; Stevens et al. 2017; Cleere 2020b). During daytime, the Egyptian Nightjar usually roosts in hidden spots, at a safe distance from the foraging areas, facilitating body temperature regulation and predator avoidance (Campbell and Smiles 2018; O'Connor et al. 2018; Wasserlauf et al. 2023). While some populations are considered migratory (Cleere 2020b), neither the generality of this pattern nor the species level of roost fidelity are well known. In Israel, the Egyptian Nightjar was previously known as a breeder, based on several observations in sandy areas along the coastal plains, until it went extinct towards the middle of the twentieth century (Paz and Eshbol 1987; Shirihai 1996). Since then, it was considered a rare migratory species, with low numbers of individuals reported annually, those were mostly observed during spring migration in the southern Arava valley (Shirihai 1996; Gancz et al. 2017). In the summer of 2016, a new population of this species was discovered in the Judean Desert, in an area adjacent to the northern shores of the Dead Sea. The consistency of the observations and the presence of juvenile individuals and family-like groups suggested that this population might be breeding in the vicinity, and even resident in the area (Gancz et al. 2017). This is despite the existing literature that suggest that this population is migratory (Paz and Eshbol 1987; Shirihai 1996).

Here, we present our study of this newly discovered population of Egyptian Nightjars (Gancz et al. 2017). A previous study investigated their behavior during the breeding season by fitting 13 individuals with tracking GPS devices (Wasserlauf et al. 2023), but the scope of the data was limited to a period of several weeks. At that time, it was unknown whether they stayed in the area beyond the breeding season or migrate elsewhere as previously suggested for the extinct coastline population (Paz and Eshbol 1987). To address this knowledge gap, we fitted Egyptian Nightjars with GPS tags (set to work for an extended period, with low-resolution sampling) to monitor their behavior during the non-breeding season. We aimed to (a) describe their long-term spatial behavior and reveal whether they show migratory or sedentary behavior and (b) investigate their roost site fidelity.

Methods and materials

Study species

The Egyptian Nightjar has a wide distribution range, stretching from Morocco in the west to Kazakhstan in the east, throughout Northern Africa and the Middle East, with some populations exhibiting migratory behavior and others remaining resident (Cleere 2020b). Due to the lack of research in the deserts of Africa and Asia, the species' current known distribution is fragmented and patchy across its wide range (Holyoak 2001; Campbell and Smiles 2018; Cleere 2020b). In this wide range, two subspecies are described: *C. a. saharae*, the African subspecies, is described in the literature as a migratory subspecies that breeds in desert and sandy habitats in North Africa, and winters in the Sahel; *C. a. aegyptius*, the Asian subspecies, with mostly migratory populations, breeds in Asia and the Middle East and winters in the Sahel (Shirihai 1996; Holyoak 2001; Campbell and Smiles 2018; Cavaillès 2019). The distinction between migratory and non-migratory populations is unclear (Cleere 2020b), with some resident populations known from Egypt, but this classification is usually based solely on field observations in familiar localities, highlighting the existing knowledge gaps in our understanding of the species ecology (Campbell and Smiles 2018; Cavaillès 2019; Cleere 2020b).

Study site

The study was conducted in the northern part of the Dead Sea area. This extreme, rain-shadowed desert with average annual precipitation of less than 100 mm is the lowest terrestrial place on earth, at a minimum elevation of 425 m below sea level. During summer, the temperature is above 40 °C for most of the day and is one of the hottest and driest areas in the eastern Mediterranean region (Israeli Meteorological Service 2024). The habitats adjacent to the Dead Sea are a mixture of exposed sandy or muddy areas, including newly exposed areas due to the retraction of the sea in the last few decades (Lazar et al. 2024). Despite being sparsely populated by humans, large areas are used for agriculture, including open fields, greenhouses and Date (*Phoenix dactylifera*) plantations.

Tagging procedure

As part of a broader study of their ecology (Wasserlauf et al. 2023), we trapped Egyptian Nightjars towards the end of their breeding season during the nights of May and June 2020. After a regular ringing and measurement procedure, individuals were mounted with a GPS tag fitted as a backpack using Teflon straps. We used PinPoint GPS-VHF 75 (Lotek Wireless Inc., UK) with a remote download capacity, through communication with a designated commander unit with a fitted antenna. Tags weighed 3.5 g, which makes up less than 5% from the Nightjars' body mass (average body mass of the five tagged individuals: 78.8 ± 6.1 g, mean ± SD). To test if individuals stay in the region year-round, we attached GPS tags to five individuals (three first year juveniles and two adults), aiming for a ten to eleven months tracking period by using settings of low GPS sampling rate that records the birds' locations twice a day: once during daytime ('day point'—at 10:00 UTC, presumably at their day-roost site) and once during their nightly activity period ('night point'—at 21:00 UTC, presumably during their foraging activity). We downloaded the data remotely at the beginning of March 2021, performing an intensive scan throughout the known activity areas and new potential areas, to ensure a broad search.

Data processing

The downloaded data was first filtered to ensure high GPS fix quality. Fixes with horizontal dilution of precision (HDOP) value higher than five (indicating poor quality) were filtered out (see Langley 1999 for details). We then calculated the distance of each 'night' point from the individual's original trapping location as well as the 'nightly displacement distances' between the individuals' roosting and foraging sites (i.e. between each 'day' point to the following 'night' point). To describe roost fidelity, we measured roost sites fidelity at two levels: at the roost site level and at the roost area level. For the site level, we aggregated all the 'day' points that were within 30 m away from each other into one diurnal roost site, for example representing a small group of bushes, that was used as a roost site. And for the roost area level we aggregated all the 'day' points that were within 200 m from each other into one diurnal roost site, representing a wider area that can be, for example, several groups of bushes in proximity to each other, sharing the same ecological properties. Next, for each individual, we numbered all the roost sites and roost areas consecutively from north to south for geographic orientation, and computed the presence at each diurnal roost and the usage (number of days) of each roost area by the specific tagged bird. Distance calculation and data analysis were done using the R package geosphere (Hijmans 2019).

Results

We obtained a total of 1144 GPS fixes from two adult nightjars (one female, weighted 84.3 g, 605 successful fixes; and one male, body mass 71.0 g, with 539 fixes), representing a tracking period of 304 and 271 days, respectively (three tagged juveniles were not relocated). During this period, the farthest point from the tagging site that each bird reached was 15.1 km, and 13.5 km, respectively. The female displaced to a maximum distance of 7 km, and the male displaced to a maximal distance of 10.9 km in a single night (Fig. 1). While the male divided his presence between close and distant areas from the tagging point, the female spent most of the time in proximity to the tagging spot (Fig. 1). The tagged nightjars also showed consistency in their nocturnal foraging areas, with many repeated movements towards the same foraging areas, resulting in distinct peaks at the density plot, showing consistent distances from the roost sites (Fig. 1).

Addressing our second question regarding roost fidelity, we found that both individuals showed strong roost fidelity. During her 304 days of tracking, the female used six different roost areas, with only ten different roost sites within them (Fig. 2a,b,d): she roosted at one area for 82% of the days (Fig. 2b), during both summer and winter, while during the autumn she roosted at four different areas in which two areas used most frequently, comprised 16% of the total tracking days. Examining the roosts at the fine-scale site level, we found a similar picture, with a single

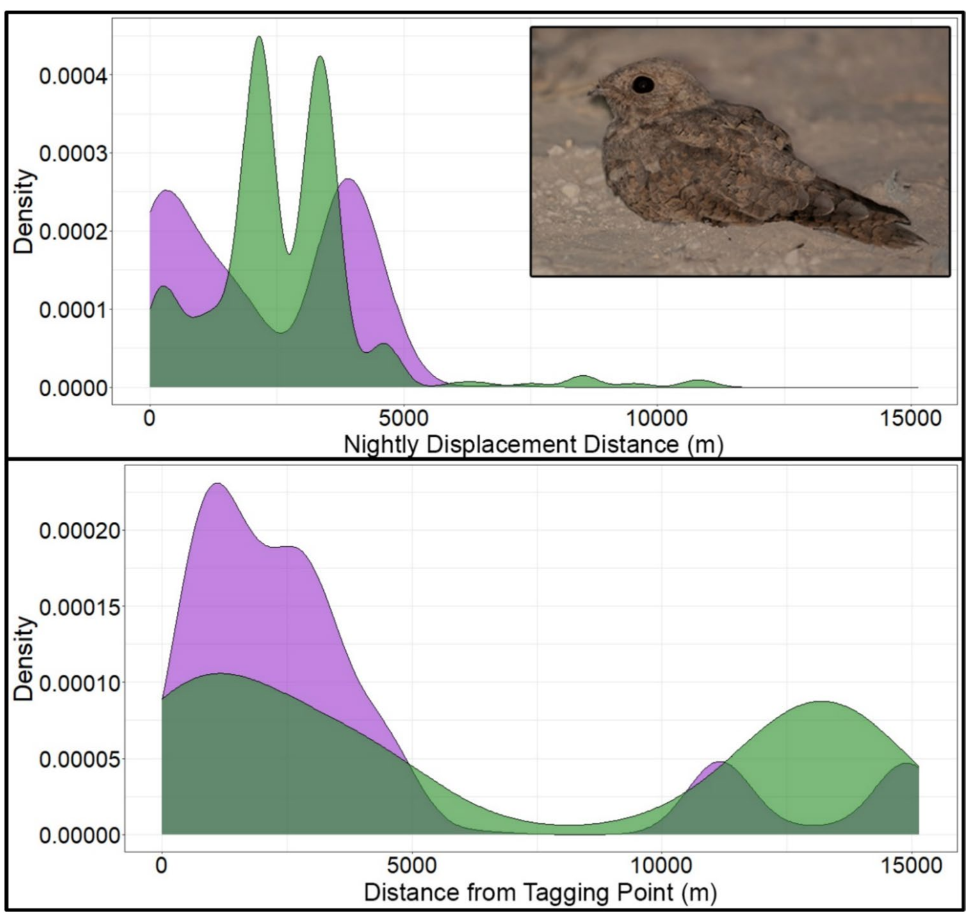

Fig. 1 Density plots for the nightly displacement from each daily roost site to the following nocturnal point (top), and from the tagging point to all the nocturnal points (bottom), for both individuals (female- purple; male-green), across all tracking days. The inset on the top right shows an Egyptian Nightjar (photographed by Yohay Wasserlauf)

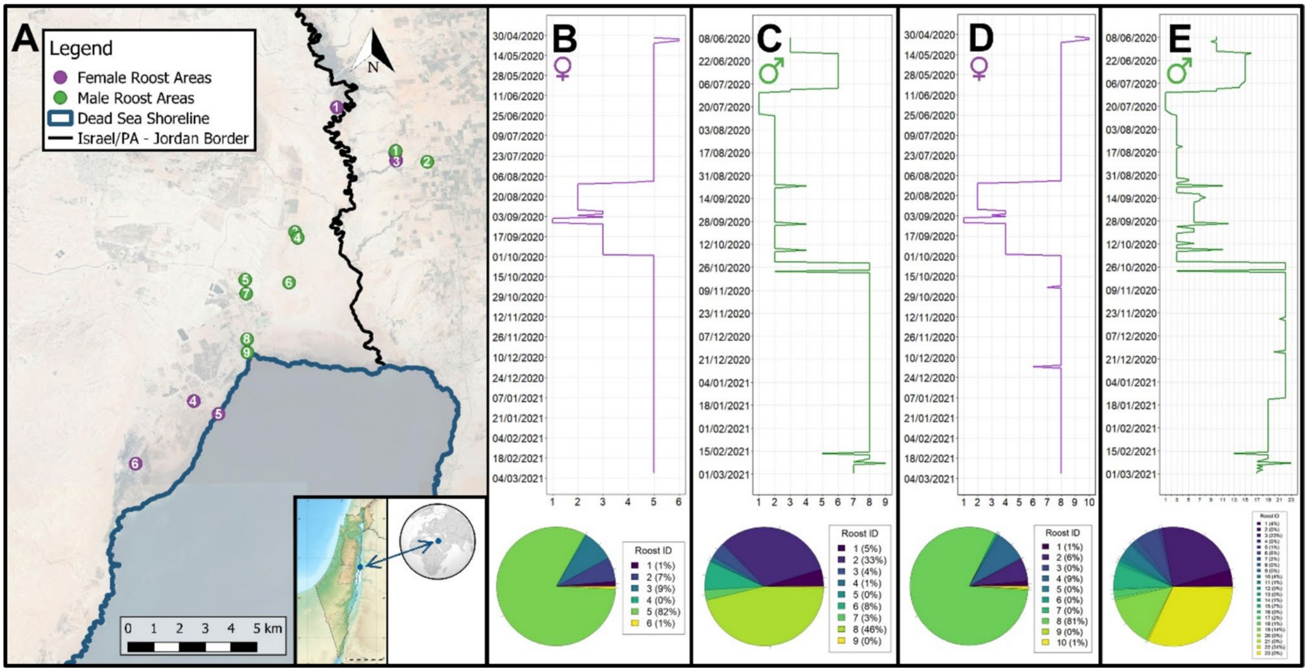

Fig. 2 Day roost usage by the two individuals (female- Purple, panels **B** and **D**; male- Green, Panels **C** and **E**). **A**: a map of the study region with the roosting areas (≤ 200 m). Roosts areas are numbered from north to south for each individual separately, note that the female's 2nd roost area is hidden under the male's first roost site. **B** and **C**: Individual's visits to each of the roosting areas, were the line marks the number of the used roost area (the X axis) by the date (y-axis), and as percentages of days (Pie-chart, bottom). **D** and **E**: Individual's visits to each of the roosting sites (≤ 30 m), were the line marks the number of the used roost point (the X axis) by the date (y-axis). The map was created using QGIS 3.4.8 Madeira (https://qgis.org/en/site) and Adobe Photoshop CS6 (https://www.adobe.com/products/photoshop.html). Small map and globe by Wikipedia, under CC BY-SA 4.0

site responsible for the vast majority of the days (#8), a couple of additional sites used for many days repeatedly (e.g. #2 and #4), and a few that were used for a single day (e.g. #6, #7 and #10; Fig. 2d).

The male used the same region and also demonstrated high roost fidelity, even if slightly lower than the female, especially notable at the fine scale. During his 271 days of tracking, he used 23 different roost sites, nested within 9 different roost areas (Fig. 2 a,c,e). In contrast to the strong dominance of one area in the female data, two main roost areas were used at a relatively similar rate, for a total of 79% of the days (Fig. 2c). Unlike the female, he also showed some seasonal variation, using the northern roost areas (and sites within them) during the summer and the autumn, and transitioning to the southern roost areas for winter (Fig. 2c,e). Apart from the two main roost areas, none of the other roost areas were used by the male for more than three weeks in total. Together, these results provide evidence of residency of Egyptian Nightjars from our focal population in the northern Dead Sea area. They also indicate year-round high roost fidelity at both scales. This is especially the case at the roost area level.

Discussion

Our results present an example of two resident adult Egyptian Nightjars at the area of the northern Dead Sea, as can concluded based on the year-round, short distance movement (Fig. 1). This represents a new status for this species in the region, where it was only known previously as a migratory bird (Paz and Eshbol 1987; Shirihai 1996; Holyoak 2001; Cleere 2020b, 2021). Further, we find a very high year-round roost fidelity with both individuals using their respective single/two main roosts for around 80% of the days (Fig. 2).

It is important to note that the three tagged juveniles were not relocated. This result may reflect either natal dispersal or partial migration by juveniles (de Greef et al. 2022), preventing us from finding them in the searched area, despite intensive surveys across a large area. Alternatively, this may reflect lower survival rates of juveniles (Wells et al. 2007) and/or premature tag failure due to harsh desert conditions. While we cannot distinguish between these non-mutually exclusive options, we note that one juvenile nightjar that was tracked over the 2019 breeding season behaved in a manner similar to the adults tracked in the same season, and remained in the same general area, at least over the two months of the tracking period (Wasserlauf et al., unpublished data). This limited data does not eliminate the possibility of natal dispersal/migration at a later date (e.g. autumn or winter) or variation of behavior among individuals (Wey et al. 2015), but may offer some support for early mortality of our tracked juveniles or premature tag failure.

As mentioned before, Nightjars differ in their migration behavior, with some species presenting migratory behavior and others known as residents (Holyoak 2001; Cleere 2021). Even within the Western Palearctic region, both of the behaviors are present. For example, the European Nightjar and the Red-necked Nightjar (*Caprimulgus ruficollis*) are migratory species, migrating between Europe and Africa (Evens et al. 2017; Norevik et al. 2019, 2025; Cleere et al. 2020b), and the Nubian Nightjar is a resident species around the rift valley (Perlman 2008; Cleere et al. 2022). Therefore, is it not unreasonable to find resident populations of Egyptian Nightjars in the deserts of the Middle East, especially with the on-going anthropogenic changes in the region facilitating constant and predictable resources year round.

Indeed, the Dead Sea area is a dynamic area and major changes can occur quite rapidly due to the human-driven, on-going retraction of the Dead Sea and the intense human development of other habitats. Notably, the establishment of agricultural fields in proximity to the Dead Sea shoreline, less than 2 km away, in the mid-1980s may have created suitable conditions for this species although it was about 30 years before an Egyptian Nightjar nest was found in the area (Gancz et al. 2017; Wasserlauf et al. 2023). With the current diversity of habitats in the Dead Sea region, it is plausible that year-round resources will be available for the Egyptian Nightjars that would support residency, as has been suggested for other systems (Gilbert et al. 2016).

The origin of our small studied population (estimated to be < 100 individuals) (Wasserlauf 2021) is still unknown. The closest known breeding area for this species is in the vicinity of the Azraq Wetland in the kingdom of Jordan, some 120 km to the east. This population is likely to belong to the Asian subspecies *C.a. aegyptius* (eBird, Cornell Lab of Ornithology, Ithaca, New York 2024). The closest known non-breeding area of Egyptian Nightjars is the Nile delta, at a distance of nearly 400 km away from the Dead Sea area, on the border between the two subspecies (Cleere 2020b). Therefore, it is difficult to establish which one of the subspecies is over-wintering in Egypt, and without genetic evidence it is not possible to determine whether they are related to the Dead Sea population.

The documented roost site fidelity, with one to two roost areas that have been repeatedly used, for about 80% of the tracking duration for both tagged individuals (Fig. 2a) aligns with other reports from various nightjar species. Several Nightjars species showed a high tendency to return to the same roost for prolonged periods (Holyoak 2001; Jetz et al. 2003; Fisher et al. 2004; Yoav Perlman 2007; Campbell and Smiles 2018; Ng et al. 2018; Tonra et al. 2019), both migratory and resident species (Norevik et al. 2025). This finding also aligns with our previous results from the breeding season, when we tracked Egyptian Nightjars for a shorter period, but with higher sampling resolution. We found that both breeding and non-breeding Egyptian Nightjars showed high roost site fidelity over the spring/breeding season (Wasserlauf et al. 2023). In this current study, the low sampling resolution facilitated longer tracking duration, documenting roost fidelity over almost a year (from the beginning of the summer to the beginning of the following spring).

We also observed some temporal changes in the roost use. It is possible that the tagged individuals were still breeding when they were tagged, which might affect their movements in the first few weeks of the tracking, until around mid-June, when breeding is completed and both parents are free from breeding duties (Holyoak 2001; Campbell and Smiles 2018). The female's persistence in the same general area for both summer and winter (Fig. 2b) might reflect stronger territorial affinity in comparison to the male (Fig. 2c), where we can describe one general area for the spring and the summer, and another general area for the autumn and the winter. Despite our limited sample size, this long-term data further underscores the importance of specific sites as a local conservation priority.

Roosting aggregations, with several individuals found at a communal roost reinforce the importance of roost sites for conservation. Such aggregations were described in other parts of the species' distribution range (Campbell and Smiles 2018), especially outside the breeding season. Communal roosts can include up to 15 individuals that can be found in one small roosting area, but also in smaller numbers of up to four individuals during the breeding season (authors personal observations). Indeed, even with the two adults here (captured independently), at least in one instance they used the same site subsequently (area #2 for the female and #1 for the male; Fig. 2a), possibly demonstrating a communal roost, with other, non-tagged individuals. Consequently, protecting these localities is especially important given the small and concentrated local Nightjars population.

Finally, in contrast to previous assumptions (Cleere 2020b), our data provide evidence for the residency and high roost fidelity of at least part of the Egyptian Nightjars population in the north Dead Sea area, adding another piece to the general puzzle of avian knowledge in the area. Admittedly, our study is limited by the available sample size, hence, even though partial migration is not known in this species (Holyoak 2001; Campbell and Smiles 2018; Cleere

2020b), this alternative should not be discharged. Greater certainty in our results will accrue from data collection over a larger area and sample size.

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Author contributions YW led the fieldwork conducted in this research, including tagging and tracking, with assistance from all co-authors. The analysis and manuscript preparation were done by YW and OS, while all authors provided valuable feedback and reviews for improving the manuscript.

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Data availability The datasets generated during and/or analysed during the current study are not publicly available due to the sensitivity of this species in the study region, but are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare that they have no conflicts of interest.

Ethical approval All capturing, ringing, and tagging procedures were carried out in accordance with the ethical regulations and procedures established by the Israeli Nature and Parks Authority (INPA). We worked under bird ringing license No. A287 and research permit No. 2019/42175, both issued by the INPA. Furthermore, the fieldwork was closely supervised by INPA rangers to ensure the project's compliance with ethical standards. The study, including all bird handling and tagging protocols, was approved by the ethical committee of Tel Aviv University.

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