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**Research Article**

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# The spatiotemporal properties of artificial feeding schemes influence the post-fledging movement of Egyptian Vultures

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## ABSTRACT

Many vulture populations have severely declined in the past decades, showing high juvenile mortality. To support these populations, feeding stations are used to increase food availability and to supply food without antibiotics and toxic compounds. Yet, supplying food at feeding stations may affect vulture behavior. We present a large-scale field experiment testing how different food provision schemes affected the movement of Egyptian Vultures (*Neophron percnopterus*). We used GPS transmitters harnessed to 18 vulture chicks and described their movements post-fledging. We categorized the vultures into 3 groups according to the feeding scheme used at feeding stations near their nests: frequent and spatially dispersed food supply (FD); non-frequent and spatially dispersed food supply (NFD); and frequent food supply, concentrated in one location (FC). We found that birds from all three groups increased their roosting distances from the nest with fledgling age, with the NFD and FC groups showing a greater increase than the FD group. Additionally, all 3 groups increased their daily flight distances, with the NFD group presenting the largest increase and the FD group presenting the smallest increase. Our findings offer new insights into the relevance of spatiotemporal differences in the management of feeding stations and show its effect on movement during birds' early life stages, creating 2 main movement patterns: local and regional. Our findings can help decide upon the preferable feeding scheme in a way that will either encourage or reduce the early dispersal distances of fledglings, according to long- and short-term conservation objectives. For example, local movements during the post fledging period to known and stable food resources may reduce the risk of anthropogenic-induced mortality, while it may negatively affect long-term survival by hindering foraging, flight, and exploring skills and affect dispersion to future breeding sites.

**Keywords:** biotelemetry, Egyptian Vulture, feeding stations, movement ecology, post-fledging period

### How to Cite

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## LAY SUMMARY

- Many vulture populations have severely declined in the past decades, showing high mortality rates among juveniles. Some of the main threats include illegal poisoning and reduction of food availability.
- To support endangered populations, feeding stations are often used as a conservation tool to increase food availability and to supply food that is clean from antibiotics and toxic compounds.
- We conducted a large-scale field experiment examining how different food provisioning schemes used in vulture feeding stations affected the development of movement behavior of fledgling Egyptian Vultures (*Neophron percnopterus*).
- We found that 3 feeding schemes and their differences in food predictability created 2 main movement patterns, local and regional. Application of an intermediate food predictability scheme resulted in juvenile birds that are more prone to local movement, as opposed to juvenile birds hatching next to high and low food predictability areas, which undertook much longer movements.
- This information reveals the effect of spatiotemporal differences in the management of feeding stations on movement during the birds' early life stage and can help decide upon the preferable feeding scheme in a way that will either encourage or reduce the early dispersal distances of fledglings, according to long- and short-term conservation objectives.

## Las propiedades espacio-temporales de los esquemas de alimentación artificial influyen en el movimiento posemplumamiento de *Neophron percnopterus*

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## RESUMEN

Muchas poblaciones de buitres han disminuido severamente en las últimas décadas, mostrando una alta mortalidad juvenil. Para apoyar estas poblaciones, se utilizan estaciones de alimentación para aumentar la disponibilidad de alimentos y suministrar alimentos sin antibióticos ni compuestos tóxicos. Sin embargo, suministrar alimentos en las estaciones de alimentación puede afectar el comportamiento de los buitres. Presentamos un experimento de campo a gran escala que prueba cómo diferentes esquemas de provisión de alimentos afectaron el movimiento de *Neophron percnopterus*. Utilizamos transmisores GPS colocados en 18 crías de buitre y describimos sus movimientos posemplumamiento. Categorizamos a los buitres en tres grupos según el esquema de alimentación utilizado en las estaciones de alimentación cerca de sus nidos: suministro de alimentos frecuente y espacialmente disperso (FD); suministro de alimentos no frecuente y espacialmente disperso (NFD); y suministro frecuente de alimentos, concentrado en un lugar (FC). Encontramos que las aves de los tres grupos aumentaron sus distancias de pernocte desde el nido con la edad de emplumamiento, siendo los grupos NFD y FC los que mostraron un mayor aumento que el grupo FD. Además, los tres grupos aumentaron sus distancias de vuelo diarias, siendo el grupo NFD el que presentó el mayor aumento y el grupo FD el que presentó el menor aumento. Nuestros hallazgos ofrecen nuevas ideas sobre la relevancia de las diferencias espacio-temporales en la gestión de las estaciones de alimentación y muestran su efecto en el movimiento durante las etapas tempranas de la vida de las aves, creando dos patrones principales de movimiento: local y regional. Nuestros hallazgos pueden ayudar a decidir sobre el esquema de alimentación preferible de manera que fomente o reduzca las distancias de dispersión temprana de los volantones, de acuerdo con objetivos de conservación a largo y corto plazo. Por ejemplo, los movimientos locales durante el período posemplumamiento hacia recursos alimenticios conocidos y estables pueden reducir el riesgo de mortalidad inducida por la actividad humana, mientras que pueden afectar negativamente la supervivencia a largo plazo al dificultar la alimentación, el vuelo y las habilidades de exploración y afectar la dispersión hacia futuros sitios de reproducción.


**Palabras clave:** biotelemetría, ecología del movimiento, estaciones de alimentación, *Neophron percnopterus*, período posemplumamiento

## INTRODUCTION

Populations of many wildlife species have declined over the past decades due to negative anthropogenic effects (Butchart et al. 2010). Notably, many vulture populations show catastrophic decline rates, with more than a third of all vulture species currently considered critically endangered (Ogada et al. 2012, Buechley and Şekercioğlu 2016, Gross 2020). Vultures encounter various threats along their life, such as direct and secondary poisoning (e.g., by farmers trying to control livestock predators), electrocution, collisions with power lines and wind turbines, reduced food availability, and habitat degradation (Shirihai 1996, Carrete et al. 2009, Donázar et al. 2010, Angelov et al. 2013, Shobrak et al. 2020). The decline in vulture populations can lead to severe negative effects on the ecosystem. These species play a crucial role in providing sanitation services by consuming carcasses and disposing of organic waste. This supports the flow of energy through food webs and enhances the health of humans, and domesticated and wild animals (Ogada et al. 2012, Gross 2020).

To overcome the demographic decline in different vulture species, and to support endangered populations, different conservation programs have been developed over the years. A common tool to conserve vulture populations is the use of feeding stations (also known as “vulture restaurants”), aiming to increase food availability (Meretsky and Mannan 1999, Donázar 2009, Donázar et al. 2010, Mateo-Tomás et al. 2019), and to provide clean and safe food (i.e., without harmful antibiotics and toxins that might be lethal to the vultures; Gilbert et al. 2007, Virani et al. 2011). Alongside the conservation advantages of feeding stations (Cortés-Avizanda et al. 2016), their use generates a fundamental change in the spatiotemporal distribution of food for scavengers. It alters 2 main characteristics of carrion: Food becomes more predictable in time and easier to find through space (Olea and Mateo-Tomás 2009, Genero et al. 2020). Therefore, applying different feeding schemes at feeding stations may substantially change vultures’ behavior (Donázar et al. 2010, Milchev et al. 2012, López-López et al. 2014,Riotte-Lambert and Weimerskirch 2013).

Changes in food distribution at feeding stations were found to influence several factors of scavengers’ ecology, such as habitat selection (López-López et al. 2014), foraging routine (Kane et al. 2016, Fluhr et al. 2017), behavior at feeding sites (Duriez et al. 2012, Cortés-Avizanda et al. 2016), and local species diversity (Cortés-Avizanda et al. 2012). However, despite the progress in understanding the implications of feeding stations’ management, its impacts on the ecology, behavior, and movement of young vultures are not well studied. Researching these impacts can be especially crucial during the early life stages of vultures, since the post-fledging period is known to have major consequences for the vultures’ fitness later in life (Wunderle 1991, Rotics et al. 2021).

The post-fledging period of birds is defined as the time between the first flight from the nest until the beginning of migration (or natal dispersal for non-migratory birds) (Davis and Fisher 2009, Jones et al. 2018). During this period, birds acquire basic skills such as flight abilities while foraging over wide, unfamiliar terrain, and becoming independent from their parents (Donázar and Ceballos 1990, Harel et al. 2016, Martens et al. 2018, Corbeau et al. 2020, Hertel et al. 2023). Moreover, skill acquisition during the post-fledging period in migrating birds may be particularly important because soon after fledging, the young birds face various threats that result in low survival during their first migration, as was recently shown for Egyptian Vultures (*Neophron percnopterus*) (Buechley et al. 2021).

The Egyptian Vulture is a relatively small avian scavenger that migrates over long distances. Its diet is based mostly on carcasses and on some small animals and excrement (Milchev et al. 2012). The Egyptian Vulture is listed in the IUCN Red List as globally endangered (BirdLife International 2021). In this study, we made use of a unique opportunity to study the effects of different temporal and spatial characteristics of food provision on the movement of young Egyptian Vultures. We used a quasi-experimental design, where food distribution was dictated by the management of food provision at feeding stations in Southern Israel. We analyzed data from GPS transmitters that were attached to 18 Egyptian Vulture chicks during 2019–2021. We tested how the spatial and temporal distribution of food at feeding stations influenced the movement and behavior of Egyptian Vultures during their post-fledging period. We predicted that young birds that hatch next to high food predictability areas, where food is supplied frequently in one place, would not rely on that main feeding station. We expected that they would fly farther from their natal area due to a possible abnormal pressure from a constant presence of Griffon Vultures (*Gyps fulvus*) (Cortés-Avizanda et al. 2012) that may monopolize this food source. This is in contrast to young birds from nests close to areas where food predictability is intermediate. We expected that, when food is supplied frequently over several different feeding stations, the young birds would fly shorter distances and use the surrounding feeding stations more frequently because of a lack of monopolization by Griffon Vultures. Furthermore, we predicted that young birds hatching in areas of low food predictability, where food is supplied irregularly in time and space, would fly the longest distances.

## METHODS

### Study Area and Feeding Stations

The Egyptian Vulture, alongside the Griffon Vulture, is 1 of 2 vulture species that currently breed in Israel, as opposed to the 5 species that bred in the region in the past (Mayrose et al. 2017). In Israel, the species is considered critically endangered, following a loss of two-thirds of its population within the last 4 decades (Mayrose et al. 2017). The study took place in the southern part of Israel (Negev and Judean Deserts, Figure 1), where the majority of the Israeli Egyptian Vulture population breeds (Mayrose et al. 2017). During the research period, 19 feeding stations were operated by the Israeli Nature and Parks Authority (INPA) in the study area. All of the feeding stations were located in open areas with no fencing, except for one in the Judean Desert, which had an ~1-m high electric fence around it, aimed to keep mammals from using the feeding station. Besides the abovementioned feeding stations, for the calculation of the number of visits at feeding stations, we also included a waste site near an agricultural settlement where dead farm animals are discarded on a regular basis.

The INPA divided the feeding stations into 6 groups according to their location, with the goal of supplying food to

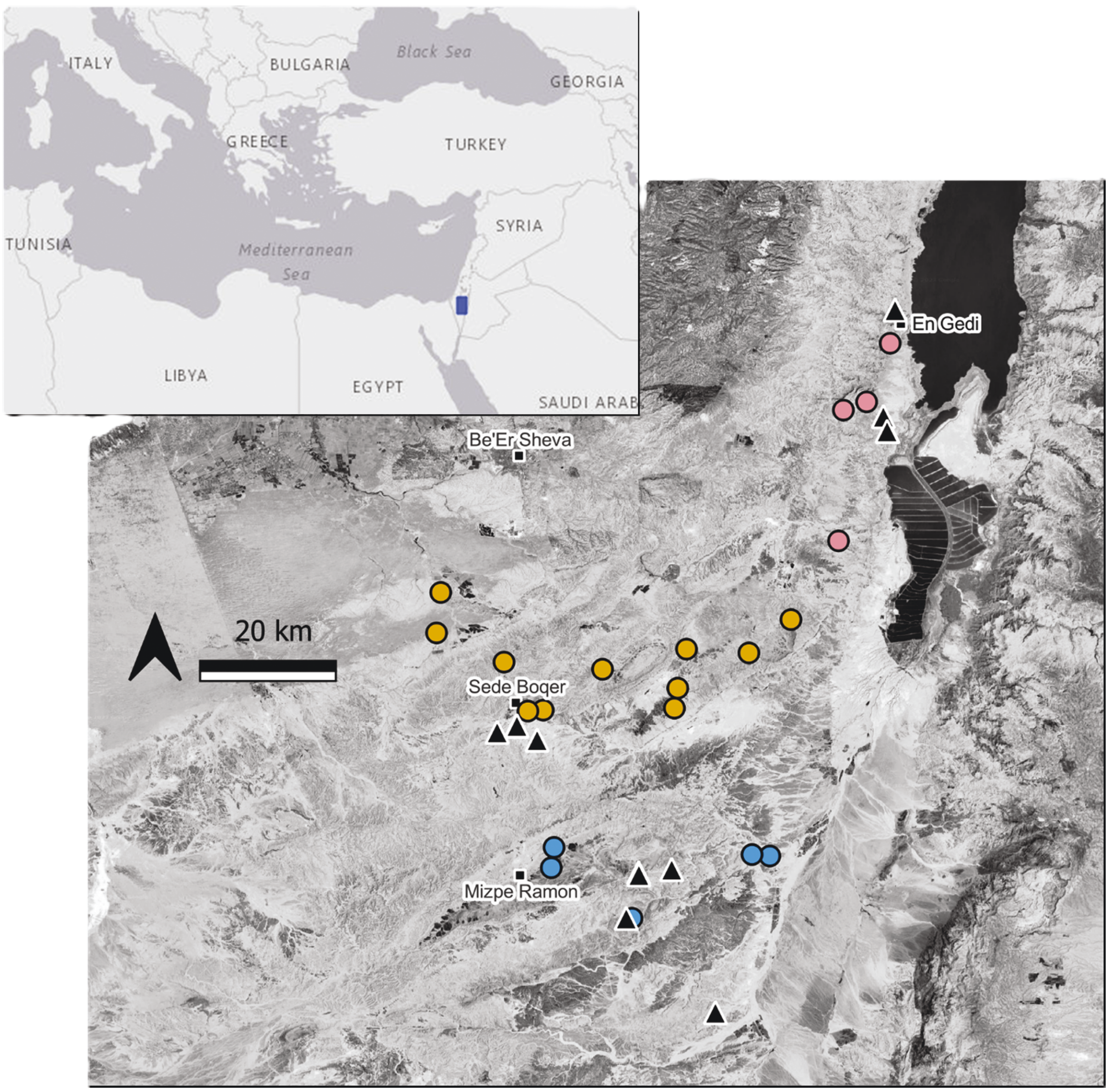


**FIGURE 1.** Map of the study area with feeding stations depicted as FD (frequently supplied and spatially dispersed, orange = 11 centered dots; including the waste site), FC (frequently supplied and central, pink = 4 northern dots), or NFD (non-frequently supplied and spatially dispersed, blue = 5 southern dots). Black triangles mark Egyptian Vulture nests in which we GPS-tagged the chicks. Inset: Mediterranean area with the study area (blue rectangle) in the south of Israel.

each of these groups throughout the year. The type of carcasses was similar across all feeding stations and included mainly domesticated animals such as cows and calves, sheep, horses, camels, and donkeys. Based on the INPA's carcass dispersion database for the years 2019–2021, during the breeding season of the Egyptian Vulture (April through mid-September), we characterized the carcass supply in each area according to its spatial and temporal properties. This allowed us to classify the 6 areas to 3 feeding scheme groups that shared similar carcass supply properties and that were geographically separated from each other (Figure 1). The carcass supply was characterized by calculating the frequency of food provision and its spatial distribution (see below; Supplementary Material Table 1). Therefore, the 3 different schemes were determined by 2 parameters: (1) the frequency of food supply in each of the three geographic areas, calculated as the mean interval, in days, that passed between consecutive feeding events in each area; (2) the level of spatial homogeneity of food distribution in each area. Spatial homogeneity describes the distribution of carcass supply in space, in terms of how dispersed or centered it is among the feeding stations of each area. High homogeneity means an even provisioning among the feeding stations of an area, in comparison to low homogeneity which means that one feeding station received most of the food, while the others were usually devoid of carcasses. Spatial homogeneity was calculated as follows. First, we computed the mean food supply frequency in each feeding station. Second, we calculated the mean and standard deviation (SD) of the food supply frequency in each area (FC area = 4 feeding stations, FD area = 11 feeding stations, NFD area = 5 feeding stations; Figure 1) using the mean food supply frequency of all feeding stations in that area. Therefore, high SD reflects low homogeneity and low SD reflects high homogeneity (Figure 2). Following these criteria, we categorized areas as: (1) FC = Frequent and Central food supply, with 4.8 ± 3.6 (mean ± SD) days between consecutive feeding events in the area, and a low level of spatial homogeneity with a standard deviation of ± 41 days among feeding events in the feeding stations. This area's feeding scheme, of frequent feeding supply with low spatial homogeneity, resulted from the provision of almost all the food in a single feeding station that was frequently supplied with carcasses. The mean distance of the nests to the feeding stations in this area was 9.4 km, and the mean minimum distance was 5.3 km. (2) FD = Frequent and Dispersed food supply, with 5.5 ± 3.5 days between consecutive feeding events, and a high level of homogeneity with a standard deviation of ± 10.5 days among feeding events in the feeding stations. The mean distance of the nests to the feeding stations in this area was 21.8 km, and the mean minimum distance was 4.3 km. (3) NFD = Non-Frequent and Dispersed food supply, with 17.6 ± 9.8 days between consecutive feeding events, and a high level of homogeneity with a standard deviation of ± 8 days among feeding events in the feeding stations (Figure 2). The mean distance of the nests from the feeding stations in this area was 25.1 km, and the mean minimum distance was 12.9 km.

Additionally, the amount of food was not equally distributed among the 3 feeding schemes during the breeding season (April through mid-September) in the years 2020–2021. Yet, because we did not have the data of the amount of food for 2019, we could not incorporate this year in our analyses. Nevertheless, we ran a two-way analysis of variance (ANOVA) that included an interaction of year (2020/2021) and feeding schemes. The result of this analysis indicated a significant difference between the feeding schemes in the amount of food provided at the stations ($F = 15.68$, df = 2, $P < 0.001$). A Tukey's honestly significant difference (HSD) post-hoc test showed a significant difference between the FC group and both the FD ($P < 0.001$) and the NFD ($P < 0.001$) feeding scheme during the year 2021. On average, during the year 2021, the FC feeding scheme was supplied with less food than the FD and the NFD feeding schemes (mean ± SE during the year 2021 of 292 ± 13 kg, 487 ± 12 kg, 537 ± 6 kg, respectively).

Apart from the difference in the feeding schemes, the 3 areas are similar in the biodiversity of wild mammals that can serve as prey, and the distribution of agricultural lands that can serve as water resources. Nevertheless, the highest breeding population of Egyptian and Griffon vultures is concentrated in the area of the FD feeding scheme, the lowest density is at the NFD feeding scheme, and the FC feeding scheme has an intermediate breeding population density (Israel Nature and Parks Authority, personal communication).

Summarizing, while vultures evolved under a context of unpredictability of food resources (periodically and scattered carcasses; Ruxton and Houston 2004), the 3 different feeding scheme categories present 3 levels of food predictability. High

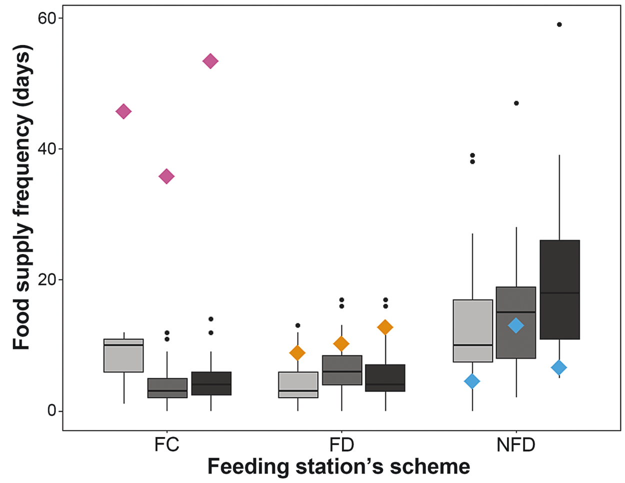


**FIGURE 2.** Food supply presented using 2 data sources in the 3 feeding schemes (FC = frequent and central, FD = frequent and dispersed, or NFD = non-frequent and dispersed). The main data depicted by boxplots are the food supply frequency in each area (FC, FD, NFD) and its standard deviation in days. Data include the years 2019–2021, from April until mid-September: 2019 = light gray = left box-plot in each group; 2020 = medium gray = middle box-plot in each group; 2021 = dark gray = right box-plot in each group. The *x*-axis shows the 3 feeding schemes and the *y*-axis presents days that passed between food supply events. The second data source, depicted by the rhombus shapes, represents the spatial homogeneity that was calculated as follows. First, we computed the mean food supply frequency in each feeding station. Second, we calculated the mean and standard deviation (SD) of the food supply frequency in each area using the mean food supply frequency of all feeding stations in that area (the rhombus aligns with the corresponding year; the color of the rhombus varies according to the feeding scheme: FC = pink; FD = orange; NFD = blue). Therefore, high SD reflects low spatial homogeneity (carcasses were supplied mainly in one feeding station) and low SD reflects high homogeneity (carcasses were supplied more evenly across several feeding stations).

predictability in FC, where food was supplied frequently and mainly in one constant feeding station; intermediate predictability in FD, where food was supplied frequently and spread across several feeding stations; low predictability in NFD, where food was supplied irregularly and spread across several feeding stations.

### Data Collection

We obtained location data from GPS transmitters (Ornitrack-30 GPS-GSM, Ornitela, Vilnius, Lithuania) during 2019–2021. The GPS tags were attached to nestlings a few weeks before they fledged, using a Teflon leg-loop harness, and weighed overall <2.5% of the birds' body mass (Bodey et al. 2018, Anderson et al. 2020). The age of each chick was determined by observations of the nest prior to tagging, and by the growth stage of the head, wing, and tail feathers which were determined while tagging the chicks. GPS measurements were collected in intervals of 10 min to 1 hr, depending on the solar-charged battery voltage. While staying in their nests, Egyptian Vulture chicks are usually not exposed to the sun and consequently, in some cases, the transmitters' battery drained and did not sample data until it was recharged. However, as the chicks left the nest, their transmitters were exposed to the sun and quickly recharged. Therefore, we do not expect that the lack of battery power before fledging substantially affected our data.

### Movement Data Analysis

We equipped 18 Egyptian Vultures with GPS-transmitters, between June 2019 and July 2021, and tracked the vultures from fledging until the onset of their seasonal autumn migration or until 35 days after fledging, if migration has not yet started (Supplementary Material Table 2). We chose to restrict our analysis to a period of maximum 35 days because the full post-fledging period was highly variable, 16–67 days. This high between-individual variability precluded comparison of the entire post-fledging period of different individuals and necessitated a more restricted, focal period to facilitate between-individual comparison (Hertel et al. 2023). Notably, the length of the post-fledging period was not related to the study groups, showing a mean length of 40.7 ± 11.8, 43.2 ± 15.6, and 29.0 ± 11.0 days for FD, NFD, and FC bird groups, respectively (one-way ANOVA, $F = 1.821$, df = 2, $P = 0.2$). All tracked birds completed their post-fledging period and started their migration.

We used GPS tracking data to quantify the vultures' movement during the first 35 days after fledging in order to estimate the influence of different feeding schemes on their movement over time. To determine the fledging date, we examined GPS locations farther than 100 m from the nest (Martens et al. 2018). We assumed that fledging would result in at least 2 sequential locations far from the nest and considered a single location farther than 100 m from the nest during an entire day as a GPS error. To further exclude potential GPS errors, we evaluated if our estimation of fledging corresponded to the known age of fledging, which is ~75 days (Ceballos and Donázar 1990, Donázar and Ceballos 1990). Migration onset was determined as the day in which a vulture flew at least 100 km to the south (the general migratory direction during autumn migration) between 2 consecutive roosting sites, after which it did not return to the nesting area (Phipps et al. 2019).

To examine the influence of the feeding scheme on the vultures' post-fledging movement range, we assigned each vulture to a group according to the feeding scheme in the area in which it hatched. The assignment area was determined by a buffer of 10 km around each vulture's nest (Hertel et al. 2023). We compared 2 movement metrics among the 3 groups: (1) the distance of the daily roosting site from the nest (hereafter roosting distances from the nest) to assess to what extent the vultures broadened their movement over new terrain; (2) the maximum distance from the daily roosting site (hereafter daily flight distance) to assess the length of their maximal daily foraging distance. In addition, apart from the movement metrics, we also compared the daily use of feeding stations. The purpose of this test was to gain a different perspective regarding this management tool, and to examine not only how it affects movement, but also how it affects the vultures' behavior in relation to reliance on artificial feeding sources. This metric was calculated as the daily number of stationary locations at all the feeding stations divided by the daily stationary locations (i.e., when the vulture was not flying). Stationary locations were classified as locations in which the GPS measured speed was < 5 km hr$^{-1}$, and a visit to a feeding station was classified when the bird was < 300 m from the feeding station (based on personal observations showing this distance can result from birds waiting near the station to feed from the carcass). We formulated 3 models to explain roosting distances from the nest, daily flight distances, and percentage of visits at feeding stations. First, we formed a generalized linear mixed effects model (GLMM) using a gamma distribution with a log link-function for the first 2 models and a binomial distribution with a logit link-function for the third model. Individual bird identities were incorporated as random intercepts. Second, to select which explanatory variables best explain the variables in question, we conducted a model selection procedure by comparing the $AIC_c$ scores across models consisting of all possible variable combinations. We considered the following variables: feeding schemes, number of days passed from fledging, their interaction, and distance of the nests from feeding station. The distance of the nests from feeding stations was tested separately from feeding scheme due to high collinearity between the 2 variables. The best model was defined as the one with the lowest $AIC_c$ score and a difference of at least 2 from the second-best model (Bartoń 2013). We report the detailed results for the top model of each of the analyses.

Data were analyzed using R software (R core team 2022), with the MuMIn and lme4 packages for statistical analyses (Bartoń 2013, Bates et al. 2015). All tests were 2-tailed with $\alpha$ of 0.05.

## RESULTS

### Movement Range

The best model of the daily roosting distance from the nest, included the feeding schemes, the days from fledging, and their interaction (Supplementary Material Table 3). The interaction term in the model indicates significant difference between the groups over days from fledging. The model's results showed that the roosting distance of the NFD and FC bird groups from the nest, over the days from fledging, increased faster than that of the FD group (Supplementary Material Table 4).

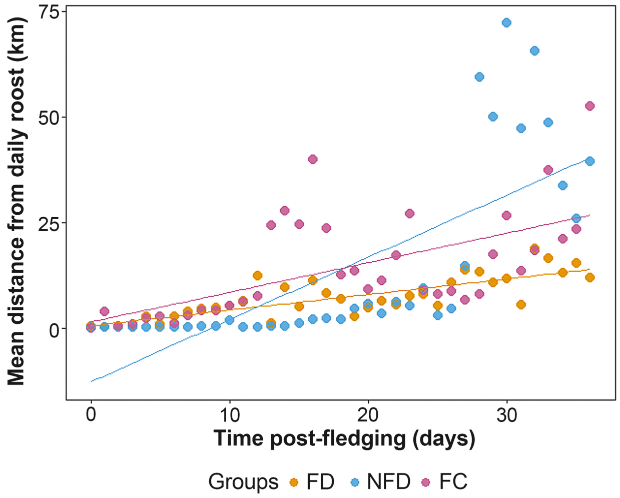


**FIGURE 3.** Raw data of the maximum daily mean flight distance from the roosting sites of 18 juvenile Egyptian Vultures during the post-fledging period. The birds are divided into 3 groups according to the temporal and spatial feeding schemes: frequent and dispersed (FD, orange = bottom line); non-frequent and dispersed (NFD, blue = middle line); and frequent and central (FC, pink = top line). The *x*-axis indicates the days from fledging such that day zero (0) is the first day of fledging. The *y*-axis presents the daily maximum mean flight distance from the daily roosting site. The dots depict the daily mean flight distance of each group and the lines represent their trends. A significant difference in flight distances over time was found for all groups.

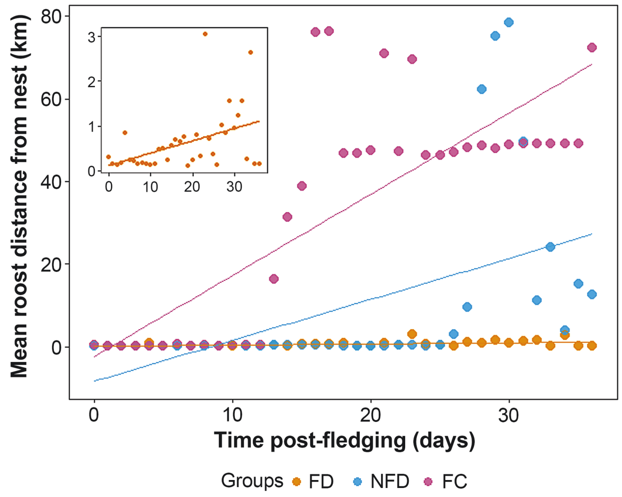


**FIGURE 4.** Raw data of the daily mean distance of roosting sites from the nest of 18 juvenile Egyptian Vultures during the post-fledging period. The birds are divided to 3 groups according to the temporal and spatial feeding scheme: frequent and dispersed (FD, orange); non-frequent and dispersed (NFD, blue); and frequent and central (FC, pink). The *x*-axis indicates the days from fledging such that day zero (0) is the first day of fledging. The *y*-axis presents the daily mean distance of the roosting sites from the nest. The inset in the upper left corner of the figure shows the roosting distance change of the FD bird group using a smaller *y*-axis scale. The dots depict the daily mean distance for each group and the lines represent their trends. A significant difference in roosting distances over time was found between the FC and NFD groups compared to the FD group.

Interestingly, the model did not suggest a notable difference in the increase rate of the daily roosting distances between the NFD and FC bird groups. This finding is noteworthy given that the mean roosting distance of the total examined post-fledging period for the FC bird group was almost three times greater than that of the NFD bird group (27 and 10 km, respectively). According to the raw data, the FC bird group began to substantially increase its roosting distance from the nest after 13 days from fledging, while the NFD bird group exhibited a boosted roosting distance change only after 27 days from the fledging date (Figure 3). In the fifth week after fledging (29–35 days), while the FC bird group stayed at more or less consistent roosting distance of at least 49 km from the nest, the NFD bird group kept changing their roosting distances at a range of 5–78 km from the nest. In comparison, the FD group birds did not perform any marked changes in their roosting distance during the examined post-fledging period and roosted at a maximal distance of three km away from their nests.

The second model examined the daily maximum flight distance from the daily roosting site. The best model included the effect of feeding schemes, days from fledging, and their interaction (Supplementary Material Table 5). The interaction of days from fledging and feeding schemes showed a significant difference between bird groups. According to the model's results, the NFD group increased its daily flight distance from the roosting sites more than the FD and FC groups. Further, the FD group increased its daily distance less than the FC group (Supplementary Material Table 6). Intriguingly, in line with the raw data, the NFD group birds began to notably increase their flight distance only on the 20th day after fledging (Figure 4). In comparison, the FD and FC bird groups greatly increased their flight distance already on the 9th and 10th day after fledging, respectively. However, in the fifth week after fledging (29–35 days), the mean daily distance of the NFD bird group from the roosting site was 2.7 and 4.7 times longer than the distance of the FC and FD bird groups, respectively. Additionally, at this time, the mean daily distance of the FC group was 1.7 times longer than the FD group.

## Visits at Feeding Stations

Out of the 463,782 total number of GPS locations, 40,841 locations were stationery, and of these, 6,468 points were within a range of 300 m from a feeding station (in this range birds were observed as waiting near the station to feed from the carcasses). Examining the percentage of visits at feeding stations, the best model included the effects of feeding schemes, days from fledging, and their interaction (Supplementary Material Table 7). The interaction term in the chosen model exhibited significant differences between groups given days from fledging. The model's results show that the FC group increased its daily visits in feeding stations faster than the FD and NFD groups, and the FD group increased it faster than the NFD group (Supplementary Material Table 8). According to the raw data, the FC bird group began to visit the feeding stations on the 5$^{th}$ day after fledging, while the FD bird group began visiting there only on the 14$^{th}$ day after fledging, and the NFD bird group did not visit at feeding station at all during the examined post-fledging period (Figure 5). The FC and FD bird groups reached the highest percentages of visits (44% and 33%, respectively) during the middle of the post-fledging period. In the fifth week after fledging (29–35 days), the mean percentage visits at feeding stations of the FC, FD and NFD groups was 23.9%, 13.1%, and 0%, respectively.

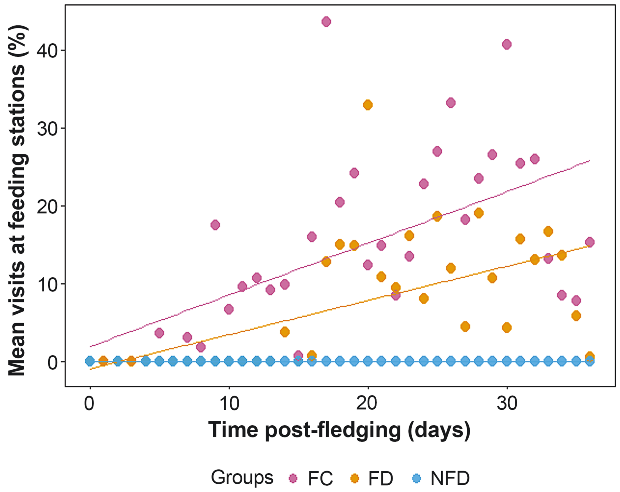


**FIGURE 5.** Raw data of the daily mean percentage of visits at feeding stations of 18 juvenile Egyptian Vultures during the post-fledging period. The vultures are divided to 3 groups according to the temporal and spatial feeding scheme: frequent and dispersed (FD, orange = middle line); non-frequent and dispersed (NFD, blue = bottom line); and frequent and central (FC, pink = top line). The *x*-axis indicates the days from fledging such that day zero (0) is the first day of fledging. The *y*-axis presents the mean percentage of visits at the feeding station. The dots depict the daily mean visits for each group and the lines represent their trends. A significant difference in feeding station visits over time was found for all groups.

## DISCUSSION

The spatiotemporal characteristics of food availability in the 3 feeding schemes reflected 3 levels of food predictability. These included a low level (NFD), where food was supplied irregularly and spread across several feeding stations; an intermediate level (FD), where food was supplied frequently and spread across several feeding stations; and a high level (FC), where food was supplied frequently, mainly in a single feeding station.

Our results show that young Egyptian Vultures increased their daily roosting distance from the nest and their daily flight distance during the post-fledging period, and that the rate of these increases was influenced by the level of food predictability in the area. As expected according to previous knowledge, all the young vultures increased their roosting distances from the nest in the days following their fledging (Hertel et al. 2023). The very act of dispersal from the nest is affected by physical body conditions and behavioral maturation, enabling the young birds to leave their natal area (Wyllie 1985, Kenward et al. 1993, Del Mar Delgado et al. 2009). However, once the physical conditions enabling dispersal have been met, dispersal behavior of non-territorial vultures can be influenced by external factors such as food availability, competition, and congregation of conspecifics and other avian scavengers (McGrady et al. 2018, Overveld et al. 2018, Serrano et al. 2021). Our results show that juveniles that hatched in an area of low food predictability (NFD) or of high food predictability (FC) tended to roost further away from their hatching areas compared to juveniles that hatched in an area of intermediate food predictability (FD). While the NFD and FC groups roosted on average 47 km away from their nest in the fifth week after fledging, the FD group remained in their local environment, roughly 1 km from their nests.

When examining the visits to the feeding stations, we found that the FD group birds visited feeding stations only in their natal area (Supplementary Material Figure 1). These findings—of the differences roosting distances and visits at feeding stations—could imply that the frequent and dispersed feeding scheme (FD scheme) discouraged young vultures from leaving their natal areas during the post-fledging period. In comparison, the frequent but concentrated food supply in the natal area of the FC group birds, and the infrequent and dispersed food supply in the natal area of the NFD group birds, seemed to encourage both bird groups to increase their roosting distances from the nest. The low level of food predictability at the NFD area possibly drove the young vultures to increase their daily flight distances in search of places with higher food availability (Kenward et al. 1993), resulting in an increased distance of the roosting sites. Interestingly, a high level of food predictability drove the birds to act in the same manner. Cortés-Avizanda et al. (2012) showed in his work from Northern Spain, that highly predictable food resources are monopolized by Griffon Vultures, which arrive earlier and in larger numbers than Egyptian Vultures to the highly predictable feeding stations. This pattern is different than the known competitive behavior in scavenger guilds, in which Griffon Vultures may arrive early but in small numbers, facilitating the feeding of other scavenger species (Cortés-Avizanda et al. 2010). Cortés-Avizanda et al. (2012) suggested that the monopolization of highly predictable feeding stations by Griffon Vultures could lead to their domination of carcasses, forcing the smaller scavenger species such as the Egyptian Vulture to consume only small pieces of food or to be completely excluded from feeding. Following these findings, the juvenile birds from the FC feeding area, which is characterized by high food predictability, may have encountered abnormal carcass monopolization by Griffon Vultures, which are the largest and the most prevalent scavenger species in our study area. Consequently, these juvenile birds might have increased their roosting distance in search of other feeding opportunities. Alternatively, the FC group birds could search for other feeding opportunities due to the lesser amount of food that was supplied in that area (total mean of 306 kg, compared to 457 and 461 kg in the FD and the NFD areas, respectively).

In addition to the increased roosting distances from the nest, we also found an increase in the daily flight distance of the young birds after their fledging. This increase is possible due to the improvement of basic functional tasks such as flight and navigation skills that come with experience, mostly during early stages of life (Bustamante 1993, Yoda et al. 2004, Ruaux et al. 2020, Efrat et al. 2023, Hertel et al. 2023). As previous works show, juvenile soaring birds improve their soaring performance to optimize their movement energetics. Thus, the juvenile birds were able to undertake longer flights and their general activity rate increased over time from fledging (Donázar and Ceballos 1990, Harel et al. 2016, Jones et al. 2018). The acquisition of these skills enables the young birds to increase their daily flight distances and expand their movement, thereby extending the distance of their foraging trips and improving their ability to find food. The increased daily flight distances also enable the birds to explore and get familiar with further, unexplored areas.

In this study, we found a difference in the rate of the daily flight distances increase between the three bird groups. The NFD bird group exhibited the longest flight distances after 29 days from fledgling, reaching a mean flight distance of 61 km, as opposed to the FC and FD bird groups that after the same time reached a mean flight distance of only 22 and 12 km, respectively. The data of visits at feeding stations reveal that the NFD group did not rely on feeding stations as a food source during the examined period. This may suggest that the low food predictability and availability characterizing the NFD area required the juvenile birds to forage over larger areas by flying longer distances in search of food. Alternatively, the distance of feeding stations from the nests might also affect the visits at feeding stations and the daily flight distances. The mean minimum distance of the feeding stations from the nests in the NFD area is 12.9 km, 2.5–3 times more than in the FC and FD areas. This fact, in combination of the low food predictability in the NFD area, might also explain why the NFD group birds did not visits feeding stations and learned to forage on natural resources. Contrastingly, the FD group which showed the shortest flight distances visited feeding stations but only in their area (Supplementary Material Figure 1). Interestingly, the FC bird group that showed a higher rate of daily flight distances increase than the FD bird group, visited feeding stations the most. These findings might be a result of the fast increase in distance from their original hatching area, while using first the feeding station in their hatching area, then rapidly exploring other food resources, expanding their daily flight distances until reaching another area with predictable food resources within the FD group natal area (Supplementary Material Figure 1). Unfortunately, we do not have comparable data from juvenile Egyptian Vultures of other populations, in order to examine which group's flight distances represents the "normal" behavior. However, nonbreeding Egyptian Vultures may reach daily distances of up to 125 km (López-López et al. 2014). Therefore, the longer flight distances of the NFD bird group are not atypical.

Which movement strategy is preferable from a management perspective? On the one hand, by increasing the distance from their natal area and their daily flight distances, Egyptian Vultures most likely encountered more diverse environments and learned to better detect food, a beneficial skill for their upcoming first migration, in which they will encounter new environments on a daily basis (Rotics et al. 2021, Hertel et al. 2023). On the other hand, juvenile birds that forage over larger areas are more prone to a variety of threats and face higher mortality risks due to their inexperience compared to adult birds, which stresses the advantage of staying close to the nest and avoiding ranging over a wider landscape. Notably, none of the tracked juveniles in our study died during their post-fledging period, which implies that the risk of exploring wider areas was not a critical factor in our study system, during this rather limited time period.

In addition to the effects of the feeding scheme, other factors that differed between the regions with the different schemes, might also have influenced movement behavior (e.g., higher nest density of Egyptian Vultures, as well as higher nest density of other species like the Griffon vulture, as found in the FD feeding scheme area; Mayrose et al. 2017, McGrady et al. 2018, Overveld et al. 2018). Avian scavengers rely on visual cues while foraging, which include gathering information from the behavior of con- and hetero-specific scavengers that are seen nearby (Mundy et al. 1992, Spiegel et al. 2013). Thereby, relatively dense populations in a certain area may attract more individuals to that place (Kane et al. 2016). While differences in climate between breeding sites or among years may affect vulture movement and behavior, we assume that this is not the case in our study system because the summer time (June to August) in the Israeli desert is characterized by a stable climate. Furthermore, we believe that our results are not affected by other geographic characteristics such as landscape, water resources and agricultural lands, as evident by data on the distribution of Egyptian Vultures from the 1980s (Mayrose et al. 2017). These data indicate similar densities across the study area, irrespective of the geographic area which remained unchanged during the past years. Notably, during this period of time, the availability of food resources substantially decreased in all of the study areas (Shirihai 1996, Mayrose et al. 2017). In conclusion, the 3 feeding schemes and their differences in food predictability created 2 main movement patterns, local and regional. Juvenile birds hatching next to an area characterized by intermediate food predictability were more prone to local movement, as opposed to juvenile birds hatching next to a high and low food predictability areas, that undertook much longer movements. Our work also shows how the management of feeding stations could shape vulture movement and behavior and by that the exploratory movement of young, endangered scavengers during their post-fledging period. These findings reveal the importance of the management of scavenger feeding stations and should encourage conservation managers to keep reevaluating and updating their programs. The management scheme of feeding stations should be determined according to new accumulating knowledge and long- and short-term objectives while considering the advantages and disadvantages of the different feeding schemes that motivate local vs. regional movements. Local movement during the post fledging period to known and stable food resources may contribute to the survival of the young birds by avoiding feeding on poisoned carcasses. It nevertheless might as well negatively affect their long-term survival by hindering their foraging and exploration skills before they embark on their first migration, heading to Africa. Regional movement, which familiraze the birds with broader areas, may lead to expansion of the breeding range in the long run, following the preliminary acquaintance of the young birds with a wider area.

## Supplementary material

Supplementary material is available at *Ornithological Applications* online.

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## Ethics statement

Trapping of vultures was done by Ron Efrat under permit 2495/2018 of the Israeli Nature and Parks Authority.

## Conflict of interest statement

The authors declare no competing interest.

## Author contributions

Korin Reznikov, Ron Efrat, Nir Sapir and Oded Berger-Tal conceived the ideas. Nir Sapir and Thomas Mueller secured the funding. Ron Efrat collected the data. Korin Reznikov analyzed the data and led the writing of the manuscript. All authors contributed to the drafts and gave final approval for publication, with input from Thomas Mueller.

## Data Availability

Data used in this study are available in the Supplementary Material file. The movement datasets are available from Reznikov et al. (2024).

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