



Trail Cameras Reveal New Details of the Breeding Behaviour of an Endangered Vulture Species

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Abstract: The Egyptian vulture (*Neophron percnopterus*) is a globally endangered species distributed in Eurasia and Africa, with a declining population in most of its range. Even though the species is well-studied, some aspects of its breeding behaviour, more precisely the share of parental care between the sexes within the pair (i.e. nest building, incubation, food provisioning), still remain poorly documented. We used trail cameras as a tool to monitor the breeding behaviour of six Egyptian vulture pairs in Bulgaria during 22 breeding attempts between 2011 and 2021. We found that the male contributes more than the female to the nest arranging ($\chi^2 = 4$, $p = 0.04$), and females participate less in nest buildings than males ($\chi^2 = 92.5$, $p < 0.05$). The rate of copulations recorded in the nest is similar throughout the years ($H = 11.95$, $df = 7$, $p = 0.1$). Both sexes seem to contribute almost equally (7.14 ± 0.126 SD hours per day on average for the female and 5.87 ± 0.123 SD on average for the male) to the incubation across the entire period ($\chi^2 = 0.125$, $p = 0.72$). Only 23% of the food delivered to the nest would be found in the remains at the end of the breeding season.

Key words: Scavenger, phenology, copulation, incubation, nest building, diet

Introduction

The Egyptian vulture *Neophron percnopterus* is a globally endangered raptor (BIRDLIFE INTERNATIONAL 2023) and one of the most studied vulture species. Many research outcomes have been directly incorporated into different conservation management actions aiming to halt the population decline of the species (CORTES-AVIZANDA et al. 2016, DOBREV et al. 2016, OPPEL et al. 2017, NIKOLOV et al. 2022, BIRDLIFE INTERNATIONAL 2023), including studies on its biology and ecology (DOBREV et al. 2016, DOBREV et al. 2021, OPPEL et al. 2021). In that context, breeding behaviour and diet represent pivotal knowledge as they can inform important conservation measures (OPPEL et al. 2016, ARKUMAREV et al. 2022). Like in any other raptor, the Egyptian

vulture's breeding cycle can be divided into five main stages: pre-laying, laying, incubation, chick-rearing and post-fledgling (NEWTON 1979). During the breeding season, the species shows high fidelity to its territories, which are used for many years, and defended from intruders (ELOSEGI 1989, CARLON 1998). In European breeding grounds, the Egyptian vulture returns from wintering around the end of March (CRAMP & SIMMONS 1980). During the pre-laying period, the main activities include nest building and copulation (NEWTON 1979). Both activities can play an important role for the breeding outcome, as they are significant effort and energy cost invested by the birds during this period (DOBREV et al. 2021). The incubation starts in April, several weeks after the return from the wintering grounds (ARKUMAREV et al. 2018). According to NEWTON (1977), the

clutch consists of two eggs (but see ANGELOV et al. 2013), which are usually laid at 2 to 4 days intervals, and then incubated for around 40–42 days by both partners (CRAMP & SIMMONS 1980, MENDELSSOHN 1983). Nevertheless, most of the studies so far have not used a robust method to detect these important events and their variations from a close distance but mostly by physical observations (DONÁZAR 1994, DOBREV et al. 2021).

The breeding adults show sexual dimorphism by the coloration of their face (NEWTON & OLSEN 1990; CLARK & SCHMITT 1998), the females having a yellow face whereas the male having an orange-yellow face. Hence, they can be easily identified based on these features. During the incubation period, females invest more energy than males, and both sexes generally invest the same effort in nestling attendance and food provisioning (ETXEBARRIA et al. 2019). However, the habits during the incubation, e.g. how the pair shares the duties (proportion of incubation time, number of switches between the partners) remain poorly documented. Furthermore, even though the partners share duties during the chick rearing, it is still unclear if this behaviour changes over the breeding season and if there is difference in the involvement of sexes. The Egyptian vulture is also an opportunistic species with a diverse diet that is using tools and hunting small preys (CRAMP & SIMMONS 1980, VAN LAWICK GOODALL 1968, DOBREV et al. 2016). The species carries food to the nest in the bill rather than by regurgitation; thus, prey remains can be used for diet analysis later (DOBREV et al. 2016). However, only sampling prey remains collected from the nest tends to overestimate larger prey species in the diet composition and thus, can lead to biased data (MARGALIDA et al. 2007, SÁNCHEZ et al. 2008). Hence, direct observation is considered the best method for an accurate and unbiased estimate of diet as it is proven to detect food items that will not be found later in the nest and are thus underestimated or neglected (MARGALIDA et al. 2007, REAL 1996). In this regard, using cameras to observe the nest can help in filling the gaps in the knowledge about diet composition (MARGALIDA et al. 2007).

This paper aims to contribute to the knowledge on the breeding behaviour and phenology of the Egyptian vulture, and more precisely revealing the parental role using motion-sensor cameras. In addition, we investigated the number of the deliveries of food into the nest and the size of the delivered food items. Likewise, we studied the difference in the amount of solid food items (bones, shells, feathers, and other diet components that can be identified after the breeding season) and soft food items (soft

tissues that leave no remains) in order to assess more accurately the food composition and the contribution of each partner to the food provisioning in the nest.

Materials and Methods

Study area

The study was carried out in the Eastern Rhodopes, Bulgaria, the core of the Balkan population of the species with about 50% of the pairs in the whole peninsula breeding there (ARKUMAREV et al. 2018, DOBREV et al. 2023). The selection of the pairs to be studied was made on two main criteria: (1) a nest occupied by a pair that have successfully bred in the previous breeding season, (2) accessibility of the nest regarding installation and maintenance of the trail camera.

Installing trail cameras

We monitored the behaviour of six pairs during their 22 breeding attempts with trail cameras between 2011 and 2021. The trail cameras were installed at the end of February – beginning of March – before the return of birds from Africa. Natural materials such as small stones taken from the nest cliff, leaves, and branches were used to camouflage the trail cameras. Boly Guard trail cameras with MMS function and Scout Guard trail cameras were used and set to take one still image when activated by movement, with a trigger interval of 30 seconds between shots. The infrared option was set off to avoid disturbance during the night. The MMS trail cameras were set to send 50 pictures daily to an email address using the GSM network. Once the cameras were installed, the targeted nests were accessed once or twice during the breeding season to change the battery pack and SD card. The first entry was made once the chicks are at least three weeks old to minimize the risk of any harm on vulture breeding (YORDANOV & DOBREV 2021). The cameras were collected between October and December. Overall, 209,224 photos were analysed.

Pre-laying period

To describe the behaviour of the birds during the pre-laying period, we focused on nest building and copulation. We also account for arrival dates and breeding outcome. For nest building, we considered the time of the day when they were involved in that activity in the first place. In this regard, we split the day into three periods: morning (A) (6:00AM – 10:00AM), midday (B) (10:00AM – 2:00PM) and afternoon (C) (2:00PM – 7:00PM). We then calculated the total time spent per partner (male and female) to arrange the nest and bring materials in or-

der to measure the contribution of each partner. We also identified all materials brought to the nest during this stage. The daily copulation frequency was estimated as copulation attempts per hour for the time-frames between 6:00AM and 8:00PM and the data for all pairs was pooled together as in similar studies (DONÁZAR et al. 1994, DOBREV et al. 2021). Furthermore, the copulation frequency was categorized (low, high) following BIRKHEAD et al. (1987).

Incubation

We analysed three aspects of the incubation behaviour:

(i) the mean time spent for incubation per individual per day, across the entire incubation period (45 ± 2.86 days);

(ii) the daily time frame (11.88 ± 0.14 hours per day) during which each partner is seen incubating through the entire incubation period (45 days / 11.88 hours per day/);

(iii) the night incubation, namely accounting for the last bird seen before dusk and the first before dawn to incubate.

Likewise, we were able to calculate how long the incubation period lasts.

Chick rearing and provisioning of food

To estimate the food composition, we classified the delivered pieces of food in the nest by their size as follows: ‘small’ (1) – a piece of food smaller than the head, ‘medium size’ (2) – a piece of food similar to the head’s size, and ‘large’ (3) – a piece of food larger than the head. As a second step, food items were also separated into the following categories: flesh (every kind of soft tissues that would not be found in the nest after the breeding season), flesh and bone, bone and unknown, with taxon identified if possible. Thus, we also account for the proportion of food that will not be later found in the nest, which might lead to misinterpreting quantities in diet studies. We also compared each partner’s contribution in to food deliveries and chick feeding to describe the feeding behaviour during the chick-rearing period.

Data analysis

We used χ^2 test to compare each partner’s contribution to the nest building, incubation and food delivery. Furthermore, we used the Kruskal-Wallis test to understand if the copulation rate was different between years, and to test if the number of male and female switches during incubation remained the same over the years. All analyses were made in RStudio – 2022.7.1.554 (R STUDIO TEAM 2020). The statistical significance was set at $p < 0.05$.

Results

The earliest date of arrival of the adults from the wintering grounds detected with trail cameras was 17th of March and the latest one was 24th of April, but in most cases 37.20% ($n=16$), the event took place between 29th March and 4th April. However, we observed two extreme cases when the male bird from the same territory for two consecutive years arrived after the first egg was laid by his early arrived partner (1st case was on 16th May, 2020 and the 2nd case was on 26th May, 2021). The earliest start of incubation was registered on 31st March and the latest on the 6th May. Nevertheless, in most of the cases – 45% ($n = 9$), the first egg was laid between 18th and 23rd of April. The two eggs were laid with an interval of 6 ± 0.49 days. The incubation of each egg continued for 41.8 ± 0.25 days. Furthermore, the earliest date of hatching of the first chick is the 20th of May and the latest date is the 6th of June, but in 53.8% of the cases ($n = 7$) this event took place between the 1st and 6th of June, with 5.4 ± 0.48 days between the hatching of both chicks. In 18 out of all 22 breeding attempts of the six pairs, 35 eggs in total were laid whereas in only one case the laid egg was just one. Furthermore, 16 of the breeding attempts (73%) were successful, 28 of the eggs hatched successfully and 25 juveniles fledged.

The nest building was taking place mainly in the morning (in 49.6% of the cases), and the contribution of the male was higher ($\chi^2= 92.5$, $p < 0.05$). The contribution of the male was also higher in the nest arrangement ($\chi^2= 4$, $p = 0.045$). Each pair delivers, on average 21.4 ± 18.4 objects per breeding season, mainly branches and wool, brought in the nest in the beak (Fig. 1).

The rate of copulation in the nest was the same throughout the years ($H = 11.946$, $df = 7$, $p = 0.1$), and the daily frequency was high (> 2 copulations per day), with most of the copulations detected either in the morning or in the afternoon (Fig. 2). Copulation was recorded for the first time in the nest on average 7.1 ± 1.9 days before the laying of the first egg and was only seen once after laying (we detected 74 copulations in nests in total).

Both sexes contribute almost equally to the incubation (7.14 ± 0.13 hours per day for the female and 5.87 ± 0.12 for the male) across the entire period ($\chi^2= 0.125$, $p = 0.72$). It seems that the female invests a bit more effort into the night incubation than the male. ($\chi^2 = 11.139$, $p < 0.05$), and the female was observed in 58.31% of the last photos before darkness and in the first picture in the morning. The number of switches between partners to incubate (136.81 ± 95.11 times on average through the incubation pe-

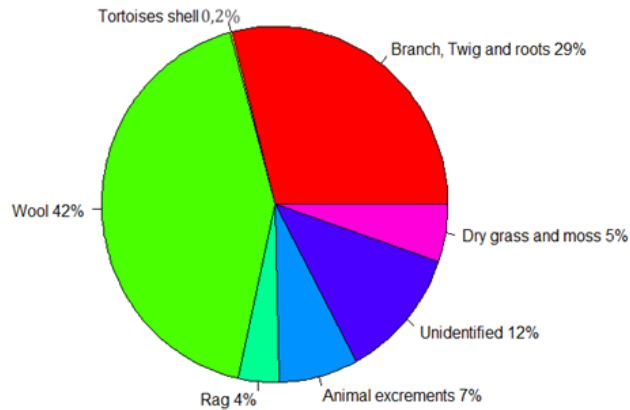


Fig. 1. The proportion of different building materials used by the Egyptian vulture for nest-building.

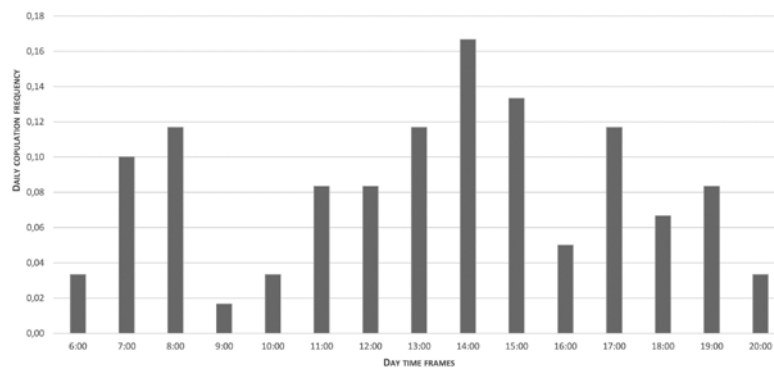


Fig. 2. The daily pattern of copulation frequencies of six pairs of Egyptian vulture during the pre-laying period (n = 74 copulations).

riod) was similar through the years ($H=5.67$, $df = 7$, $p = 0.57$). The total number of switches for the entire study period for all breeding pairs was 2189. In total, 78.90% ($n=1727$) of the switches are made in the nest and 21.10% ($n=462$) are made outside of the nest.

The total number of food deliveries throughout the entire study period was 816, and in 751 cases, the items' size could be identified (Fig. 3).

Of the delivered 638 food items identified with the trail cameras, "soft tissues" represented 65%, "bone and flesh" and "bone" represented 13% and unidentified taxa 22%. The food deliveries are shared almost equally between the partners ($\chi^2= 1.32$, $p = 0.25$), and during the chick-rearing period, the chicks were fed at similar rates by the male and the female ($\chi^2 = 1.35$, $p = 0.24$). For the entire study period, the total number of registered feedings for all studied pairs was 2,064.

Discussion

As in many other migratory birds, the Egyptian vulture is optimizing its spring migration to return as early as possible to occupy its breeding territory

(NILSSON et al. 2013). In our study, the earliest occupation date of a nest was the 17th of March, and the latest arrival of an adult in a nest – 26th of May. Generally, the adult Egyptian vultures in the Balkans return from their wintering grounds in a wide range of time, and as early as the middle of March as in the current study (PHIPPS et al. 2019). The arrival dates of Egyptian vultures in the breeding territory might vary because of weather conditions and individual qualities of the birds or other factors (LOPEZ-LOPEZ et al. 2014, AGOSTINI et al. 2015). Furthermore, the significant variation of the arrival dates could also be explained by the high level of variability at the individual level exhibited by the species in the Balkans regarding basic migration parameters (PHIPPS et al. 2019). In accordance with other studies (CRAMP & SIMMONS 1980, ARKUMAREV et al. 2018), we confirm that in most of the cases incubation starts between the 18th and 23th of April and the incubation period lasts 41.8 days. The Egyptian vulture is a species that usually lays two eggs (BROWN & AMADON 1968, CRAMP & SIMMONS 1980, NAOROJI 2006), of which one usually hatches (NAOROJI 2006). Our results support

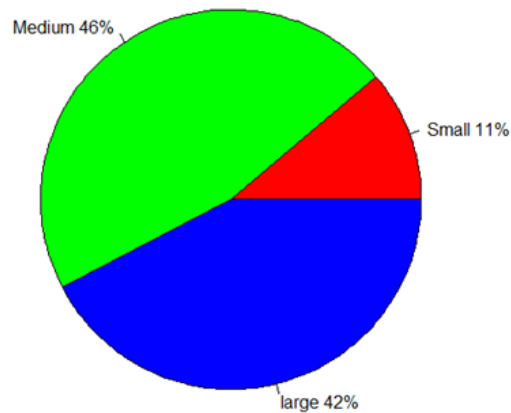


Fig. 3. The proportion of different in size food items delivered to the nest: small (84), medium (349) and large (318 cases).

these findings. Furthermore, as in other studies we registered 73% of the breeding attempts as successful (ARKUMAREV et al. 2018). Using trail cameras to detect the duration of incubation and breeding outcome could be also applied widely in other species in order to support conservation management programs (NIKOLOV et al. 2022).

During the pre-laying period, the Egyptian vulture is mostly involved in courtship behaviour and nest building, similarly to many other raptor species (NEWTON 1979, MARGALIDA & BERTRAN 2000). The data on nest building behaviour in raptors is generally scarce and this behaviour is poorly studied (NEWTON 1979). In our study, the nest-building activity started around 15.1 ± 7.7 days before egg laying. It is performed mainly in the mornings like in other vultures (MENDELSSOHN & LESHEM 1983, MUNDY et al. 1992) and in contrast to the Bearded vultures (*Gypaëtus barbatus*) known to start building nests months before laying (MARGALIDA & BERTRAN 2000). Our results evidence that the male Egyptian vulture has the major role in nest building and arrangement, as in other vulture species (MARGALIDA & BERTRAN 2000). This is most likely a demonstration of their reproductive abilities (MARGALIDA & BERTRAN 2000). Nest-building behaviour of males provides females with information about the quality of their mates (SOLER et al. 1998). The nest material is carried in the beak (DONÁZAR 1993) as observed in the current study too. We confirmed that wool is mostly used to line the nest, and materials such as different branches, twigs and roots are used to strengthen the structure (ORTA et al. 2020). Given the fact that nest building and repair can be a significant effort and energy drain for those involved (COLLIAS & COLLIAS 1984), this behaviour of less activity on the part of females will help them avoid excessive energy drain, which would affect the optimal physical condition

required for successful reproduction (MARGALIDA & BERTRAN 2000).

Although Egyptian vulture is considered to copulate outside the nest, with the current study, we support recent findings that this happens very often in the nest too (DONAZAR et al. 1994, DOBREV et al. 2021). We report that first copulations start on average 7.1 ± 1.9 days before laying the first egg, and daily frequency is high, with peaks between the peaks of copulations observed outside the nest (DOBREV et al. 2021). The high frequency of copulation both in and outside the nest could be explained by the attempts of the male to ensure paternity and to dilute the sperm of possible competitors, as copulations of the female with other males are possible (BIRKHEAD et al., 1987, DONAZAR et al. 1994). Given the fact that we confirm that the species copulates actively in the nest, except for reproductive purposes, copulations in the nest might also play a role in strengthening and maintaining the partnership between the two birds (NEGRO & GRANDE 2001, DOBREV et al. 2021).

The incubation in raptor species is considered as essentially held by female birds (NEWTON 1979). Our results demonstrate that the male and the female contribute at similar rate to the incubation, and the frequency of switches is high, with more than 137 per season. Nevertheless, it seems that the female is laying over the eggs during the night in most cases. This could be explained by the slightly larger size of the females, which could better secure the temperature for the eggs on one hand and should be able to repel intruders more efficiently on the other (NEWTON 1979). Even no evident difference in size between the sexes is visible in the Egyptian vulture, most of the females are slightly larger and heavier in size compared to the males (BSPB, unpublished). The majority of the switches between the partners that we registered are made inside the nest. This is

most probably related to the time optimization and the urge of the birds to cover the eggs and not leave them exposed to diverse weather conditions and other factors (ZUBEROGOITIA et al. 2014).

The Egyptian vulture is an opportunistic scavenger whose diet has been studied in some parts of its range including Bulgaria (MILCHEV et al. 2012, DOBREV et al. 2016). Nevertheless, identifying the diet of a raptor species is always challenging (SIMMONS et al. 1991). In contrast with some eagles (DEMERDZHIIEV et al. 2022), identifying the composition of the Egyptian vulture's diet, and particularly identifying what proportion of it consist of soft tissues and what of items that can be later found in the nest (solid food items) is difficult (DOBREV et al. 2021). This is important as can give an idea about the type of food delivered on one hand, and the habits of the birds on the other. The development and application of new technologies create opportunities to look closer into such details (YORDANOV & DOBREV 2021). In the current study most of the food items (65%) are soft tissues which will not be found later in the nest and thus the proportion of this type of food will be underestimated or unknown (DOBREV et al. 2016). This detail has an important application as usually the soft tissues origin from larger carcasses, which are more likely to be poisoned. This is especially valid in areas where the human-predator conflict is severe (SKARTSI et al. 2014). Hence, evidence about these specific feeding habits of the pairs is particularly important. For example, the proportion of these types of food items that they deliver to the nest can help to answer questions regarding their main feeding habits and sources of food, namely, if they visit vulture feeding sites, collect road kills, hunt on small prey, etc. (DOBREV et al. 2016). Hence, based on that, targeted conservation measures could be undertaken for these pairs to support their survival (OPPEL et al. 2016). This methodical approach can be used in other fragmented and small populations of the species to identify the feeding habits of different pairs, thus eventually suggesting specific targeted conservation actions for them. This could be especially important for remnants of the population of the species throughout the different clusters in the Balkans for example (VELJEVSKI et al. 2015). However, in order to understand the overall composition of the diet, to identify the different specimen, the trail cameras method during breeding should be combined with the method of searching for food residues after the breeding period. The results from our study show that most of the food items that the birds bring to the nest are the size of the head or bigger. The Egyptian vulture usually feeds on dead carcasses or visits dumpsites or other food

sources. This requires mobility and well-adapted diet habits, during the chick-rearing period. Considering the presence of competitors on the feeding sites, the Egyptian vulture should be able to pick and transport enough amount of food to the nest easily. This could most probably explain the results in our study showing that most of the deliveries to the nest are made with medium-sized or large food items. This is also related with the chick rearing and the feeding of the chicks, which we proved to be almost equally held by both parents.

The use of trail cameras is a very good method for better understanding the birds' breeding behaviour. It can be helpful for more precise characterisation of breeding parameters, e.g. arrival date, date of laying, date of hatching, size of the clutch, etc. In addition, it is a good tool for establishing the quantity of the delivered food and the rate of copulation in the nest throughout the years. Generally, the better knowledge of the phenology and quantity of the delivered food of the species can be useful in organizing various conservation practices. These include supplementing feeding of the breeding couples to provide them with enough food for successful rearing offspring. Furthermore, being familiar with the fledgling period will allow conservationists to organise nest-guarding initiatives. This can aid in reducing chick mortality and, thus, support the population (DOBREV & NIKOLOV 2021, OPPEL et al. 2016).

Installing trail cameras in the Egyptian vulture nests can be a challenge. Furthermore, if not done correctly it may cause disturbance to the birds and thus, can lead to abandonment of the nest. From our experience, we have learned that there are ways to avoid any of this disturbance. Here, we outlines some of the practices we use while installing the cameras:

(1) The trail cameras should be installed before the start of the breeding season and masked in the best possible way, using natural materials.

(2) If the nest is built in a small niche (height > 95 cm, depth > 100 cm, width >120 cm), the trail cameras should not be placed/mounted inside it. In these cases, no matter how well the camera is masked, it will disturb the breeding pair, which can lead to them dislodging the nest.

(3) In case of a small nest niche, the camera is to be placed outside of the nest. If not possible, no camera shall be installed.

(4) If placed outside, the distance from the nest should not exceed 4m. Otherwise, the motion sensor will rarely detect movements, which will significantly reduce the number of photos taken during the day. However, because the camera is further away from the nest the sensitivity should be set on 'high'.

(5) In the nest, the cameras should be as well camouflaged with natural materials as possible, It is recommended to use small stones from the rock on which the nest is located.

(6) Materials such as wool are not recommended because in strong winds it peels off or can activate the motion sensor. Birds also pull it.

(7) It is best to use rechargeable UPS batteries. One UPS battery lasts one season for one camera. Using rechargeable batteries saves producing additional waste each season.

(8) Memory cards (SD Cards) should be 32GB (or 64 GB if trail camera specifications allow) to ensure that the SD cards do not fill up before the end of the breeding season.

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References

- AGOSTINI N., PANUCCIO M., & PASQUARETTA C. 2015. Morphology, flight performance, and water crossing tendencies of Afro-Palaearctic raptors during migration. *Current Zoology*, in press.
- ANGELOV I., YOTSOVA T., SARROUF, M. & MCGRADY M.J. 2013. Large increase of the Egyptian Vulture *Neophron percnopterus* population on Masirah Island, Oman. *Sandgrouse* 35: 140–152.
- ARKUMAREV V., DOBREV V., STOYCHEV S., DOBREV D., DEMERDZHIEV D. & NIKOLOV S. C. 2018. Breeding performance and population trend of the Egyptian Vulture *Neophron percnopterus* in Bulgaria: conservation implications. *Ornis Fennica* 95(3): 115–127.
- ARKUMAREV V., SARAVIA-MULLIN V., DOBREV V., DOBREV D., KLISUROV I., BOUNAS A., IVANOVA E., KRET E., VAIDL A., OPPEL S. & NIKOLOV S. C. 2022. Reinforcement Strategy for the Egyptian Vulture (*Neophron percnopterus*) in Bulgaria and Greece. Technical report under action C3 of the LIFE project “Egyptian Vulture New LIFE” (LIFE16 NAT/BG/000874). Bulgaria, 76 p.
- BERTRAN J. & MARGALIDA A. 1999. Copulatory behavior of the bearded vulture. *Condor* 101: 164–168. doi: <https://doi.org/10.2307/1370459>.
- BIRKHEAD T.R., ATKIN L., & MØLLER A.P. 1987. Copulation behaviour of birds. *Behaviour* 101(1–30): 101–138. doi: 10.1163/156853987X00396.
- BIRDLIFE INTERNATIONAL. 2023. Species factsheet: *Neophron percnopterus*. Downloaded from <http://www.birdlife.org> on 19/03/2023
- BROWN L. & AMADON D. 1968. Eagles, Hawks and Falcons of the World. Hamlyn, London, 432 p.
- CARLON J. 1998. Resurgence of Egyptian Vultures in western Pyrenees and relationship with Griffon Vultures. *British Birds* 91: 409–416.
- CLARK W. & SCHMITT N. 1998. Ageing Egyptian Vultures. *Alula* 4: 122–127.
- COLLIAS N. E. & COLLIAS E. C. 1984. Nest Building and Bird Behaviour. Princeton University Press, Princeton.
- CORTÉS-AVIZANDA A., BLANCO G., DEVAULT T. L., MARKANDYA A., VIRANI M. Z., BRANDT J. & DONÁZAR J. A. 2016. Supplementary feeding and endangered species: benefits, caveats and controversies. *Frontiers in Ecology and the Environment* 14: 191–199.
- CRAMP S. & SIMMONS K. 1980. Birds of Europe, the Middle East and North Africa. Vol II. Oxford University Press, Oxford.
- DEMERDZHIEV D., BOEV Z., DOBREV D., TERZIEV N., NEDYALKOV N., STOYCHEV S., & PETROV T. 2022. Diet of Eastern Imperial Eagle (*Aquila heliaca*) in Bulgaria: composition, distribution and variation. *Biodiversity Data Journal* 10: e77746. <https://doi.org/10.3897/BDJ.10.e77746>
- DOBREV V., BOEV Z., ARKUMAREV V., DOBREV D., KRET E., SARAVIA V., BOUNAS A., VAVYLIS D., NIKOLOV S.C. & OPPEL S. 2016. Diet is not related to productivity but to territory occupancy in a declining population of Egyptian Vultures *Neophron percnopterus*. *Bird Conservation International* 26: 273–285 doi:10.1017/S0959270915000155
- DOBREV V., YORDANOV E. & POPGEORGIEV G. 2021. Copulatory behaviour of the Egyptian vulture (*Neophron percnopterus*) in the Eastern Rhodopes, Bulgaria. *Ecologia Balkanica* 13 (1): 9–16.
- DOBREV V. & NIKOLOV S. 2021. Supplementary feeding and nest guarding of the Egyptian vulture in Bulgaria (2017 – 2020). Technical report under action D1 of the Egyptian Vulture New LIFE project (LIFE16 NAT/BG/000874). Plovdiv, 13 p.
- DOBREV V., OPPEL S., WESTON J., SARAVIA-MULLIN V., ARKUMAREV V., NIKOLOV S.C. & THE LIFE PROJECT TEAM. 2023. Monitoring the impact of LIFE project activities on Egyptian Vulture populations along the flyway. A report under actions D1 and D3 of the LIFE project “Egyptian Vulture New LIFE” (LIFE16 NAT/BG/000874). BSPB, Sofia, 44 p.
- DONÁZAR J.A. 1993. Los Buitres Ibéricos: Biología y Conservación. J. M. Reyero (ed.), Madrid.
- DONÁZAR J.A., CEBALLOS O. & TELLA J.L. 1994. Copulation behaviour in the Egyptian Vulture *Neophron percnopterus*. *Bird Study* 41: 37–41.
- DZHAMIRZOEV G. & BUKREEV S. 2009. Status of Egyptian Vulture *Neophron percnopterus* in the North Caucasus, Russian Federation. *Sandgrouse* 31 (2): 129–133.
- ELOSEGI I. 1989. Vautour fauve (*Gyps fulvus*), Gypaète barbu (*Gypaetus barbatus*), Percnoptère d’Égypte (*Neophron percnopterus*): Synthèse bibliographique et recherches. *Acta Biologica Montenegrina. Serie Documents de Travail*, 3.
- EXTEBARRIA J.M., LÓPEZ-LÓPEZ P. & ARROYO I. 2019. Parental investment asymmetries of a globally endangered scavenger: unravelling the role of gender, weather conditions and stage of the nesting cycle. *Bird Study*, <https://doi.org/10.1080/00063657.2019.168825>
- GIOVANNI M., BOAL C. & WHITLAW H. 2007. Prey use and provisioning rates of breeding Ferruginous and Swainson’s hawks on the southern Great Plains, USA. *The Wilson Journal of Ornithology* 119(4): 558–569.

- ÍÑIGO A., BAROV B., ORHUN C. & GALLO-ORSI U. 2008. Action plan for the Egyptian Vulture *Neophron percnopterus* in the European Union. Brussels: BirdLife International and European Commission.
- LOPEZ-LOPEZ P., GARCIA-RIPOLLES C. & URIOS V. 2014. Individual repeatability in timing and spatial flexibility of migration routes of trans-Saharan migratory raptors. *Current Zoology* 60: 642–652.
- MARGALIDA A. & BERTRAN J. 2000. Breeding behaviour of the Bearded Vulture *Gypaetus barbatus*: minimal sexual differences in parental activities. *Ibis* 142 (2): 225–234.
- MARGALIDA A., MAÑOSA S., BERTRAN J. & GARCÍA D. 2007. Biases in studying the diet of the Bearded Vulture. *Journal of Wildlife Management* 71: 1621–1625.
- MENDELSSOHN H. & LESHEM Y. 1983. Observations on reproduction and growth of Old World Vultures. In: WILBUR S.R. & JACKSON J.A. (eds.): *Vulture Biology and Management*. University of California Press, Los Angeles, pp. 214–241.
- MILCHEV B., SPASSOV N. & POPOV V. 2012. Diet of the Egyptian vulture (*Neophron percnopterus*) after livestock reduction in Eastern Bulgaria. *North-Western Journal of Zoology* 8: 315–323.
- MUNDY P., BUTCHART D., LEDGER J. & PIPER S. 1992. *The Vultures of Africa*. London: Academic Press
- NAOROJI R. 2006. *Birds of Prey of the Indian Subcontinent*. Om Books International, India.
- NEGRO J. & GRANDE M. 2001. Territorial signalling: a new hypothesis to explain frequent copulation in raptorial birds. *Animal Behaviour* 62: 803–809. doi: 10.1006/anbe.2001.1811.
- NEWTON I. 1977. Breeding strategies in birds of prey. *The living Bird*, 16.
- NEWTON I. 1979. *Population ecology of raptors*, T & A D Poyser, London.
- NEWTON I. & OLSEN P. 1990. *Birds of Prey*. Golden Press, Sydney, 240 p.
- NIKOLOV S.C., DOBREV V., ARKUMAREV V., DOBROMIR, D. & IVANOVA E. 2022. Egyptian vulture (*Neophron percnopterus*) Action plan in Bulgaria 2023–2032. MEW, Sofia. (In Bulgarian).
- NILSSON C., KLAASSEN, R.H. & ALERSTAM T. 2013. Differences in speed and duration of bird migration between spring and autumn. *American Naturalist* 181: 837–845.
- OPPEL S., DOBREV V., ARKUMAREV V., SARAVIA V., BOUNAS A., KRET E., SKARTSI T., VELEVSKI M., STOYCHEV, S. & NIKOLOV, S. C. 2016. Assessing the effectiveness of intensive conservation actions: Does guarding and feeding increase productivity and survival of Egyptian Vultures in the Balkans? *Biological Conservation* 198: 157–164.
- OPPEL S., DOBREV V., ARKUMAREV V., SARAVIA V., BOUNAS A., MANOLOPOULOS A., KRET E., VELEVSKI M., POPGEORGIEV G. S. & NIKOLOV S. C. 2017. Landscape factors affecting territory occupancy and breeding success of Egyptian Vultures on the Balkan Peninsula. *Journal of Ornithology* 158: 443–457.
- OPPEL S., BUECHLEY E.R., LÓPEZ-LÓPEZ P., PHIPPS L., ARKUMAREV A., BOUNAS A., WILLIAMS F., DOBREV V., DOBREV D., STOYCHEV S., KRET E., CECCOLINI G., SARAVIA V AND NIKOLOV S.C. 2021. Egyptian vulture *Neophron percnopterus*. In: PANUCCIO, M., MELLONE, U. & AGOSTINI N. (Eds.) *Migration Strategies of Birds of Prey in Western Palearctic*. CRC Press, pp. 22–34.
- ORTA J., KIRWAN G. M., CHRISTIE D. A., GARCIA E. F. J. & MARKS J. S. 2020. Egyptian Vulture (*Neophron percnopterus*), version 1.0. In *Birds of the World* (del Hoyo J. et al., Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. <https://doi.org/10.2173/bow.egyvvul1.01>
- PHIPPS W. L., LOPEZ-LOPEZ P., BUECHLEY E.R., OPPEL S., ALVAREZ E., ARKUMAREV V., BEKMANSUROV R., BERGER-TAL O., BERMEJO A., BOUNAS A., ALANIS I.C., D LE PUENTE J., DOBREV V., DURIEZ O., EFRAT R., FRECHET G., GARCIA J., GALAN M., GARCIA-RIPOLLES C., GIL A., IGLESIAS-LEBRÍJA J.J., JAMBAS J., KARYAKIN I.V., KOBIERZYCKI E., KRET E., LOERCHER F., MONTEIRO A., ETXEBARRIA J.M., NIKOLOV S.C., PEREIRA J., PESKE L., PONCHON C., REALIHO E., SARAVIA V., SEKERCIOGLU C.H., SKARTSI T., TAVARES J., TEODOSIO J., URIOS V. & VALLVERDU N. 2019. Spatial and temporal variability in migration of a soaring raptor across three continents. *Frontiers in Ecology and Evolution*, doi:10.3389/fevo.2019.00323.
- PIEROTTI R. 1981. Male and female parental roles in the Western Gull under different environmental conditions. *The Auk* 98(3): 532–549.
- REAL J. 1996. Biases in diet study methods in the Bonelli's eagle. *Journal of Wildlife Management* 60: 632–638.
- RSTUDIO TEAM 2020. RStudio: Integrated Development for R. RStudio, PBC, Boston, MA URL
- SÁNCHEZ R., MARGALIDA A., GONZÁLEZ L.M. & ORIA J. 2008. Biases in diet sampling methods in the Spanish Imperial Eagle *Aquila adalberti*. *Ornis Fennica* 85: 82–89.
- Şen B., TAVARES J.P. & BILGIN C.C. 2017. Nest site selection patterns of a local Egyptian Vulture *Neophron percnopterus* population in Turkey. *Bird Conservation International*.
- SIMMONS R., AVERY D. & AVERY G. 1991. Biases in diets determined from pellets and remains: correction factors for a mammal and bird-eating raptor. *Journal of Raptor Research*, 25: 63–67.
- SKARTSI T., DOBREV V., OPPEL S., KAFETZIS A., KRET E., KARAMPATSA R., SARAVIA V., BOUNAS T., VAVYLIS D., SIDIROPOULOS L., ARKUMAREV V., DYULGEROVA S. & NIKOLOV S. C. 2014. Assessment of the illegal use of poison in Natura 2000 sites for the Egyptian Vulture in Greece and Bulgaria during the period 2003–2012. Technical report under action A3 of the LIFE+ project “The Return of the Neophron” (LIFE10 NAT/BG/000152). WWF Greece, Athens. 75 p.
- SOLER J. J., CUERVO U., MILLER A. P. & DE LOPE E. 1998. Nest building is a sexually selected behaviour in the Barn Swallow. *Anim. Behav.* 56: 1435–1442.
- VAN LAWICK GOODALL J. 1968. Tool-using bird: the Egyptian Vulture opens Ostrich eggs. *National Geographic* 133: 630–641.
- VELEVSKI M., NIKOLOV S. C., HALLMANN B., DOBREV V., SIDIROPOULOS L., SARAVIA V., TSIKIRIS R., ARKUMAREV V., GALANAKI A., KOMINOS T., STARA K., KRET E., GRUBAČ B., LISIČANEC E., KASTRITIS T., VAVYLIS D., TOPI M., HOXHA B. & OPPEL S. 2015. Population decline and range contraction of the Egyptian Vulture *Neophron percnopterus* on the Balkan Peninsula. *Bird Conservation International* 25(4): 440–450.
- YORDANOV E. & DOBREV V. 2021. Guidelines for installing trail cameras in nests of Egyptian vultures (*Neophron percnopterus*) in Bulgaria. Under action D1 of the LIFE project “Egyptian Vulture New LIFE” (LIFE16 NAT/BG/000874). BSPB, Plovdiv. 10 p.
- ZUBEROGOITIA I., ZABALA J., MARTÍNEZ J. E., GONZÁLEZ-OREJA J. A. & LÓPEZ-LÓPEZ P. 2014. Effective conservation measures to mitigate the impact of human disturbances on the endangered Egyptian vulture. *Animal Conservation* 17: 410–418.

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