Biology of Tropical Birds

Nesting behavior, egg morphology, and breeding biology of Harwood's Spurfowl (*Pternistis harwoodi*) in the Upper Blue Nile Basin, Ethiopia

Comportamiento de anidamiento, morfología de huevos, y biología reproductiva del Francolín de Harwood (*Pternistis harwoodi*) en la Cuenca Alta del Nilo Azul, Etiopía

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ABSTRACT. This study aims to understand the life history of the endemic Harwood's Spurfowl (*Pternistis harwoodi*) including reproductive, behavioral, and spatio-temporal variability of traits for the first time in the Upper Blue Nile Basin, Ethiopia. We used field observations and camera traps to collect data from August to December 2020. We observed a non-lekking polygyny mating system, with females selecting the nesting sites. Most nests were designed to thwart predators through background matching, nest orientation and positioning, and reducing depositional odor trails. We found that the peak egg-laying period occurred in the first 2 wks of October. There were significant differences of clutch-size variation spatiotemporally, as well as variation of the geometrical parameters of eggs spatially, excluding for shape index. The average hatching success was 4.12 chicks/nest (± 0.91 SD). The daily nest survival rates (DSR) were estimated at 98.82% ± 0.003 (95% CI: 98.31%–99.32%), and the total survival probability of the nests was 70.48% ± 0.01 (95% CI: 60.66%–81.82%). We document a uniparental care strategy, with eggs being exclusively incubated by females and chicks being predominantly attended by their mothers, although males may support rearing the chicks during the post-hatching period.

RESUMEN. Este estudio tiene como objetivo entender por primera vez la historia de vida del endémico Francolín de Harwood (*Pternistis harwoodi*), incluyendo la variabilidad reproductiva, comportamental y espacio-temporal de rasgos en la Cuenca Alta del Nilo Azul, Etiopía. Usamos observaciones de campo y trampas cámara para colectar datos desde Agosto a Diciembre 2020. Observamos un sistema de apareamiento de poliginia sin lekking, con las hembras seleccionando los sitios de anidamiento. La mayoría de los nidos fueron diseñados para confundir a los depredadores mediante la imitación del fondo, la orientación y posicionamiento del nido, y reduciendo los rastros de olores por deposición. Encontramos que el pico del periodo de puesta de huevos ocurrió en las primeras 2 semanas de Octubre. Existieron diferencias significativas en la variación espacio-temporal del tamaño de la nidada, como también variación espacial de los parámetros geométricos de los huevos, excluyendo el índice de forma. El éxito de eclosión promedio fue de 4.12 pichones/nido (± 0.91 DS). Las tasas de sobrevivencia diaria de los nidos (DSR) fueron estimadas en 98.82% ± 0.003 (95% IC: 98.31%–99.32%), y la probabilidad de sobrevivencia total de los nidos fue de 70.48% ± 0.01 (95% IC: 60.66%–81.82%). Documentamos una estrategia de cuidado uniparental, con los huevos siendo incubados exclusivamente por las hembras y los pichones siendo atendidos predominantemente por sus madres, sin embargo los machos pueden apoyar en la cría de los pichones durante el periodo posterior a la eclosión.

Key Words: *background matching; breeding biology; daily nest survival rates; egg morphology; nesting behavior; parental care*

INTRODUCTION

The breeding biology of most tropical bird species is poorly known (Xiao et al. 2017, Fierro-Calderón et al. 2021), yet the knowledge of it is an indispensable tool to carry out successful conservation measures (Green 2004, Kesler et al. 2018). For example, knowing the details of the breeding biology of landfowl (Galliformes) can help mitigate negative influences on the populations (e.g., hunting, habitat loss, and human population growth) when taken into consideration during the development of appropriate management plans (Clark et al. 1999, Jiménez and Conover 2001, Tian et al. 2018). Nest-site selection and nest design are among the most important determinants of reproductive success in birds (Mainwaring et al. 2014, Guillette and Healy 2015), which is reflected in ground nesters like galliforms by the interplay of resource availability, thermoregulation, crypticity, and risk avoidance behaviors (Mayer et al. 2009, Carroll et al. 2015, Gömez et al. 2019).

Galliformes mostly select nest sites on the ground to build scrape nests (Madge and McGowan 2002). Scrape nests are structurally weak, but require less effort to build (Suárez et al. 2005, Mainwaring et al. 2014) than the burrow and mound nests of megapodes (Harris et al. 2014), yet great parental attention is invested during egg laying, incubation, and hatching (Persson and Göransson 1999, Suárez et al. 2005). However, there is a paucity of information on how such a nest confers reproductive success in many galliform species.

Globally, there are 54 genera in the family Phasianidae, seven of which (*Xenoperdix*, *Afropavo*, *Peliperdix*, *Campocolinus*, *Scleroptila*, *Margaroperdix*, and *Pternistis*) are confined to Africa (Gill et al. 2024). There is limited information on the breeding biology of most species, including francolins and spurfowls, from Sub-Saharan Africa (del Hoyo et al. 1994, Madge and McGowan 2002), with some studies only reported from South Africa (e.g., Little and Crowe 1993, Jansen 2001, van Niekerk 2001, 2017,

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2018). In Ethiopia, Harwood's Spurfowl (*Pternistis harwoodi*) is an endemic sedentary species of the Sudan-Guinea Savanna biome and of the Afrotropical Highlands biome, excluding the Afroalpine and sub-Afroalpine ecosystems (Abrha et al. 2023). The main threats to these biomes are agricultural expansion, livestock grazing, firewood collection, and settlement (Asefa et al. 2020), whereas the main menacing factors for francolins and spurfowls in Ethiopia are habitat loss and hunting pressure (Töpfer et al. 2014, Abrha et al. 2017, Gedeon et al. 2017, Abrha et al. 2023).

Some aspects of the ecology of Harwood's Spurfowl have hitherto been studied in the Jema and Jara Valley sub-basins of the Upper Blue Nile Basin (Robertson et al. 1997, Abrha and Nigus 2017, Abrha et al. 2017, Abrha et al. 2018). From a life history standpoint, only a single egg-laying date and a polygamous mating system have previously been reported (Ash 1978, Robertson et al. 1997, Ash and Atkins 2009), so its breeding biology basically remains elusive. This study investigates the behavior and breeding biology of Harwood's Spurfowl for the first time. Specifically, it aims to understand life-history traits, such as reproductive (clutch size, egg geometrics, incubation, brood size, daily nest survival rates, breeding success, hatching failure, and related traits) and behavioral (nest-site selection and design, social behavior, mating system, and parental care) traits, as well as spatiotemporal variation among traits.

METHODS

Study area
The study area lies in the Upper Blue Nile Basin (UBNB; Fig. 1) and consists of two main study sites separated by a distance of approximately 100 km. The main vegetation types are Dry evergreen Afromontane forest and grassland complex (DAF) and *Combretum-Terminalia* woodland and wooded grasslands (CTW) (Friis et al. 2010). The common native tree species are *Combretum* spp., *Terminalia* spp., *Acacia* spp., and *Juniperus* spp. The CTW also harbors socio-economically important plants such as frankincense (*Boswellia papyrifera*) and lowland bamboo (*Oxytenanthera abyssinica*) (Friis et al. 2010). According to Fishpool and Evans (2001), the lower elevations (mean = 1322 m, range = 840–1941 m, *N* = 27 nests) of the study area belong to the Sudan-Guinea Savanna biome (SG), whereas the higher elevations (mean = 1712, range = 1245–2192 m, *N* = 65 nests) are part of the Afrotropical Highlands biome (AH) (Figs. 1, 2). The study areas do not contain Afroalpine and sub-Afroalpine ecosystems as defined by Töpfer and Gedeon (2020). The major soil types of the area are Vertisols ("black cotton soils") and Leptosols ("gray-brown or brown soils") (Last 2009). The main rainy season in the area is from June to September, and occasional showers occur in October (Mohammed et al. 2022).

Field methods
We searched for nesting sites from mid-August to the last week of December in 2020 along predetermined line transects in farmland, CTW, and DAF habitats (Abrha et al. 2023). We intensively searched in the morning and evening, when the species exhibits peak feeding and calling activity (Abrha et al. 2018). In particular, the distinctive vocalizations of territorial males were important signals, as were courtship displays. Incubating birds were detected by random searches in habitats where the species

was known to breed (Fig. 3). An active scrape was considered as a permanent nesting site when it contained at least one egg during that breeding season. Females squatting on freshly scraped ground were also considered as signs for a potential nest.

In total, we found 119 nests in the two biomes (27 in SG; 92 in AH). We collected complete data from 92 nests (referred to as "measured nests"). For the remaining 27 nests ("unmeasured nests"), we only documented clutch size, nesting period (backdated), nest fate (successful and failed), and nest dimensions in order to understand the effect of nest visits on the breeding success of the species. A nesting period is defined as the time from the first egg laying until hatching, and a nest was considered successful when at least one egg hatched (Klett et al. 1986, Steenhof and Newton 2007). We checked 79% of measured nests in 2–3 d intervals and 21% of the nests in intervals of 4–5 d. We installed camera traps to investigate breeding activity in 40 nests in the eastern study site in AH biome (Append. 1). Camera traps were situated at a 2–3 m radius from the nests after clutch initiation in order to avoid nest desertion. All cameras were mounted on short trees or wooden stakes approximately 40–60 cm above the ground. Cameras were programmed to operate during incubation and hatching. We set cameras to take photos and enabled video mode for three consecutive days; finally, each day was pooled into a single survey following Kross and Nelson (2011). Using these methods, we were able to observe the frequency of egg laying during morning and evening, egg-laying intervals (number of egg/ day), trips to and from the nest, nest attendance during feeding activity (time/day), hatching (time) and vocalizing males and potential predators.

Nest site characterization
During our field work, we collected four traits to characterize the nest microhabitat as follows:

1. Background matching: we captured digital photographs from overhead to document the contrast between the birds' plumage color and the background. In order to minimize disturbance, a minimum distance of 1 m between the observer and the female was assumed during photographing.

2. Nest orientation and positioning: exposure to extreme weather conditions (e.g., solar radiation, rainfall, and wind) and slope gradient (gentle to steep) was determined as "oriented" or "non-oriented." Furthermore, the presence or absence of vegetation cover and nesting in association with other bird species was visually assessed.

3. Nest dimensions: we measured internal diameter, external diameter, and depth of both measured and unmeasured nests and we identified the different nesting materials after hatching.

4. Nest spacing: We applied GPS to assess the minimum nest spacing between two nests and distance between a territorial male and the nearest nest.

Geometrical parameters and coloration of eggs
Egg dimensions and mass of fresh eggs were gauged in the field using digital calipers (to the nearest 0.01 mm) and digital balances (to the nearest 0.01 g), respectively. Egg measurements were conducted when females had left the nests for foraging or after

Fig. 1. Study area and the two main study sites of Harwood's Spurfowls in the Upper Blue Nile Basin (UBNB): western nests belong to the Sudan-Guinea Savanna biome (SG) and eastern nests to the Afrotropical Highlands biome (AH).
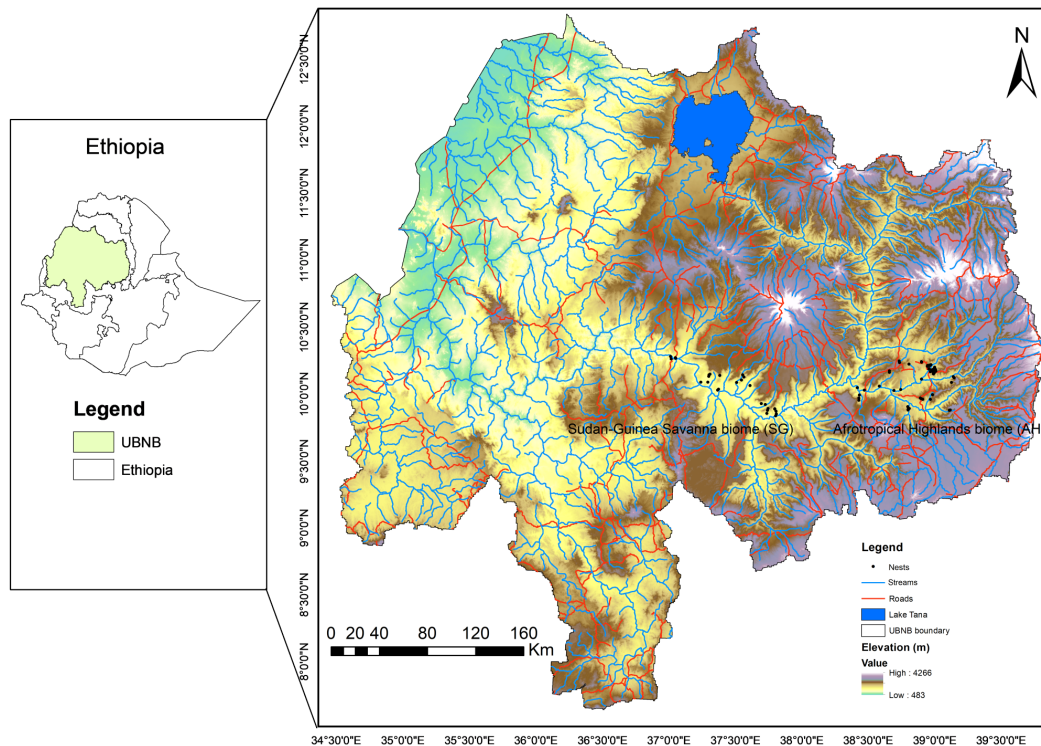

Fig. 2. Habitat types in the Afrotropical Highlands biome (top) and the Sudan-Guinea Savanna biome (bottom) in the Upper Blue Nile Basin.

antipredator responses. We wore gloves during measurements to reduce our scent on the eggs in order to avoid the attraction of mammalian predators common in the study area. We calculated the egg shape index, surface area, and volume from two egg parameters: maximum length (L) and maximum breadth (B). The egg shape index (SI) was computed as a percent ratio of egg breadth and egg length (B/L*100) (Preston 1968). Egg volume was calculated using the equation in Hoyt (1979). Based on the modified Hügelschäffer's model with two parameters (Narushin

et al. 2022), the formula for Kv coefficient for an ovoidal egg shape is: $Kv = -0.0012(B/L)^2 + 0.0035B/L + 0.5115$, where Kv = specific mass coefficient of egg. The detailed formulae for both egg surface area and egg volume are given in Narushin et al. (2022).

We dichotomized dominant phenotypic egg traits for egg color as being white or dusty white with tiny white spots and egg texture as being smooth and partly smooth (Append. 2).

Data analysis
We checked the normality assumptions of our data using a Shapiro-Wilk test and homoscedasticity to apply appropriate statistical tests. Adhering to these assumptions: (1) we applied paired and unpaired sample t-tests to contrast the mean differences of fresh eggs laid per nest between morning and evening time blocks and nest measurements between successful and failed nests, respectively; (2) we used Pearson's correlation test to check the linear relation between geometrical egg parameters; (3) the ordinary least squares (OLS) regression method was used to analyze the relationship between clutch size and egg-laying dates; (4) we also used nonparametric tests such as Chi-Square (χ^2) Goodness of Fit test, Mann-Whitney test U, and Kruskal-Wallis test H. The Chi-Square test was used to contrast the observed and expected distribution of nest orientation, egg color, and texture of eggs. The Mann-Whitney and the Kruskal-Wallis tests were used to analyze spatiotemporal variation of egg biometrics and hatching success between measured and unmeasured nests. A post hoc Dunn's test with Bonferroni error adjustment method was used for pairwise

Fig. 3. Nesting sites of Harwood's Spurfowls on relatively flat terrain in farmland (A–C) and on a steep slope in DAF (D). Nest locations proper are highlighted by white-dashed circles. Nests are effectively covered by vegetation (partly placed aside for photography) and are positioned and oriented to avoid excessive exposure to weather conditions and disturbances. Images also show effective camouflaging against the background substrate.

comparisons of each parameter between habitats. Data were analyzed with IBM SPSS Statistics v20.0. Data of life-history traits were presented as mean ± SD, and a two-tailed hypothesis test with an alpha value of 5%.

Because not all nests were encountered simultaneously, nest fate (i.e., successful = 0 and failed = 1) of Harwood's Spurfowls were derived from daily nest survival rates (DSR) in program MARK (White and Burnham 1999, Dinsmore et al. 2002). Accordingly, we calculated 95% CI of DSR (Eq. 1) and total nest survival probability (or breeding success) using a maximum likelihood estimation. Mayfield's (1975) formula for DSR is:

$$DSR = 1 - \frac{\text{Number of failed nests}}{\text{Number of exposure days}} \qquad (1)$$

The "exposure days" are defined as the duration from the first nest observation until the final fate of nests. The overall probability of a nest survival rate of d days is DSR^d, where, "d" refers to the summation of egg-laying and incubation periods (Mayfield 1975, Rotella et al. 2004) in our model species.

RESULTS

Social behavior and mating system
Harwood's Spurfowl is sympatric with Erckel's Spurfowl (*Pternistis erckelii*) at higher elevations in AH and with Helmeted Guineafowl (*Numida m. meleagris*) at lower elevations in CTW and farmlands. Male Harwood's Spurfowls were territorial and interacted with domestic and wild animals (Fig. 4A–C). Constant

territorial calls of individual males were noticed throughout the breeding season. We observed males to produce territorial calls during the mornings (6:00–11:00) and afternoons (15:00–18:30). In a continuous habitat, four to eight males were calling at a distance of approximately 90 m from each other. Within each of these individual territories, we found at least two nests. On average, males were recorded at a distance of 23.6 m away from incubating females (14.5–45.0 m, N = 23 nests). Average distances between nests were 30.1 m in farmland (14.5–52.0 m, N = 22 nests), 39.1 m in CTW (19.0–70.0 m, N = 8 nests), and 48.7 m in DAF (32.0–66.0 m, N = 3 nests). There was no significant difference of nest spacing between habitat types (Kruskal-Wallis test H = 4.30, df = 2, P = 0.07). Most nests were constructed in and around farmlands (60.87%, N = 56), followed by CTW (31.52%, N = 29 nests) and DAF (7.61%, N = 7 nests). According to our observations of five sites, the mating system of Harwood's Spurfowl is polygynous. During the season, individual males chased down several females and initiated courtship behavior before nest building mainly after mid-August in 2020. We never observed a lekking system.

Nest-site selection and nest-building behavior
Nests were inconspicuous and usually well hidden in herbaceous vegetation with some short trees and often surrounded by rocks and stones. Most nests were found on black cotton soil adjacent to stones (60.86%, N = 56), as well as underneath overhanging rocks (18.48%, N = 17 nests) and under thorny and bushy vegetation (11.96%, N = 11 nests) (Fig. 5). The gray-brown to dark-brown vermiculated patterns and colors of the breeding females' plumage matched the background very well. Only eight

Fig. 4. A territorial male feeding in association with Common Duiker *Sylvicapra grimmia* (A) and domestic goats *Capra* sp. (B), but fled from the feeding ground and gave off warning calls when approached by predators like White-tailed Mongoose *Ichneumia albicauda* (C). Males scratch the ground to feed, dust-bathe, and preen their bodies during quiescence, as indicated by remaining feathers (D).

nests (8.70%) were built in heaps of *Sorghum* stalks, where females were less camouflaged. Females usually remained motionless during photography (Figs. 3, 5). Many nests were oriented away from excessive exposure to weather conditions like sunlight, rainfall, and strong wind (63.04%, *N* = 58 nests), being sheltered by an extensive vegetation cover and by the selection of slopes and rocks on microhabitat levels (Fig. 3). There was a statistically significant difference between the observed and expected distribution of nest orientation in the study area (χ^2 = 31.34, df = 1, *P* < 0.001).

The nest itself is placed in a flat scrape and consists of a structurally weak arrangement of dried grasses and thin twigs, lined with the females' down or other soft body feathers (Fig. 5). Green plant material was not observed in any nest, and our videos confirmed that females selectively plucked and incorporated dried twigs and grasses to the construction while crouched low on the nest. The average external and internal diameters of the nests were 19.94 ± 1.76 cm and 16.85 ± 1.81 cm (*N* = 40 nests), respectively. The average depth of nests was 6.20 ± 1.43 cm. There was no significant difference in external diameter between successful and failed nests (unpaired-*t* = 1.565, df = 38, *P* = 0.126). Similarly, there was no significant difference in depth of successful and failed nests (unpaired-*t* = 0.370, df = 38, *P* = 0.714). In contrast, successful nests were significantly wider in internal diameter (1.4 cm) than failed nests (unpaired-*t* = 2.529, df = 38, *P* = 0.016).

Egg laying and egg description
On average, in each nest, a single egg was laid per day (mean = 1 d, range = 0–2 d, *N* = 23 nests) and the average egg-laying span was 8.34 d (± 2.87, range = 3–13 d, *N* = 41 nests). Our results showed that there was a statistically significant difference in eggs laid between morning and evening (paired-*t* = 5.21, df = 30, *P* < 0.001). The earliest clutch initiation was recorded on 9 September 2020, and the latest was recorded on 29 December 2020, with 52.20% of the clutches initiated in October (peaking in the first 2 wks of October). There was a linear relationship, indicating that clutch size declines significantly from the start of the laying season to the end (R^2 = 0.11; F = 6.786, df = 1,57, *P* = 0.012) (Fig. 6). The color of 67.39% of the eggs was white, and 32.61% were dusty white. Egg texture was either rough (73.91%) or smooth (26.09%) (Fig. 5; Append. 2). There were significant differences in egg color (χ^2 = 11.13, df = 1, *P* = 0.001), as well as in egg texture (χ^2 = 21.04, df = 1, *P* < 0.001) across nests.

Geometrical parameters of eggs and spatiotemporal variation of clutch size
Egg measurements were conducted on 224 fresh eggs (54.63%) from 66 nests. Fresh eggs weighed on average 25.20 g (± 1.74). The average egg length and breadth were 42.13 mm (± 0.86) and 32.95 mm (± 0.73), respectively. The average egg volume and surface area were 23.35 cm³ (± 1.31) and 34.12 cm² (± 1.23), respectively. The average shape index was 78.25% (± 1.79). Across habitat types, most egg parameters showed significant differences, except for egg shape index (Kruskal-Wallis test *H* = 0.78, *P* = 0.677) (Table 1). The average clutch size was 4.46 eggs/nest (± 1.09, range = 2–7, *N* = 410 eggs from 87 nests), with a modal clutch size of four eggs. Pearson correlation showed a significant positive association between most parameters. Only egg length showed a significant negative association with shape index, and mass and surface area did not show significant associations with egg shape index (Append. 3). Clutch size showed significant differences across habitats (Kruskal-Wallis test *H* = 13.95, *P* = 0.001), biomes (Mann-Whitney test *U* = 443.5, *P* < 0.001), and months (Kruskal-Wallis test *H* = 12.99, *P* = 0.003) (Table 2).
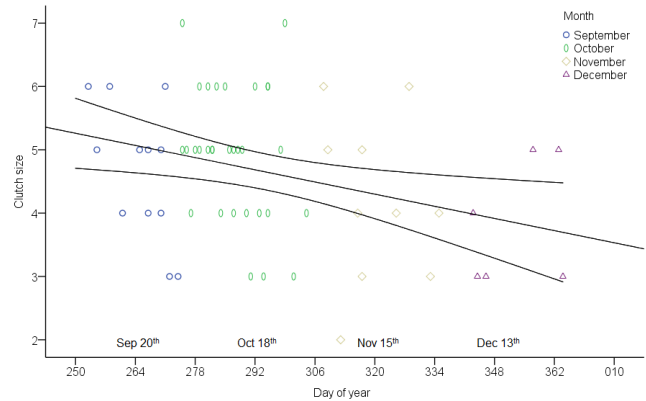
Fig. 5. Examples of nest structure and composition in different habitat types. The color and patterns of the incubating females provide camouflage against the background of rocks, stones, and soil. Typical nest sites are shown on black (A) and brown-to-gray brown soils (B), and underneath rocks (C and D). Egg colors ranged from white (A, C, and D) to dusty white with tiny white spots (B). Nests with eggs close to hatching were usually filled with soft down feathers (C).

Fig. 6. Linear relationship between clutch size and egg-laying dates of Harwood's Spurfowls ($N = 59$), indicating clutch size to decline significantly with laying date. The line fit is mean with 95% CI. $y = -0.33x + 5.35$: y = clutch size and x = days passed after the first egg laid.

Incubation, hatching, and parental care

Based on our 3-d nonstop video recordings, only females incubated the eggs. The average incubation lasted for 20.81 d ($\pm$ 1.09, 19–23 d, $N = 36$), and 66.67% of the eggs were incubated for 20 and 21 d. Additionally, the videos documented that females were never provisioned with food by males, but left their nests unattended, likely in search of food (mean 74.71 $\pm$ 38.90 min/day, 11–188 min, $N = 108$ observations), which corresponded to 5.19% of their daily time budget ($\pm$ 0.02%, range = 0.76–13.06%). Videos from farmland nest sites showed that females sometimes foraged directly from seeds of grasses covering the nests. Females left the nests for feeding frequently in the morning and in the evening, with higher activity observed in the morning (Mann-Whitney test $U = 213$, $P < 0.001$). The average nesting period for measured and unmeasured nests was 29.36 d ($\pm$ 3.51, 22–35 d, $N = 36$) and 31.53 d ($\pm$ 1.81, 26–33 d, $N = 19$ nests), respectively. Hatching was synchronous and lasted on average for 137.27 min ($\pm$ 79.44, 68–

298 min, $N = 11$ nests). Usually only females were present during hatching, although in four nests (5.3%) both sexes fed chicks in the nest during the post-hatching period.

Breeding success and hatching failure

Out of 92 nests, we evaluated the fate of most measured nests ($N = 78$ nests, 84.78%). Accordingly, 73.08% ($N = 57$ nests) were successful, and 26.92% ($N = 21$ nests) failed. Only 14 nests (15.22%) were censored due to extreme weather conditions, logistical constraints, and accessibility. Among the successful nests, all eggs (100%) hatched in 23 nests. Altogether 235 chicks hatched, of which seven chicks (2.99%) were found dead in and around seven nests during our last nest visit, possibly due to adverse weather conditions. The average hatching success was 4.12 chicks/nest ($\pm$ 0.91, 2–6 chicks), which was equivalent to 86.94% ($\pm$ 11.60) chicks/nest in measured nests. In these nests, the DSR was estimated at 98.82% $\pm$ 0.003 (95% CI: 98.31–99.32%), and total nest survival probability (DSR^d) was 70.48% $\pm$ 0.01 (95% CI: 60.66–81.82%) (Table 3). The average hatching success for the unmeasured nests was 5.22 ($\pm$ 0.80, 4–7 chicks) or 95.47% ($\pm$ 7.88) chicks/nest. The DSR and nest survival probability were 99.45% $\pm$ 0.003 (95% CI: 98.92–99.99%) and 84.14% $\pm$ 0.01 (95% CI: 71.00–99.61%), respectively (Table 3). Our results showed that unmeasured nests had higher hatching success than measured nests (Mann-Whitney test $U = 380$, $P = 0.002$).

The status of 38 eggs from 34 nests was categorized as unhatched (47.37%), collected (23.68%), disappeared (21.05%), and rolled out of nest (7.89%) (Table 4). Human footprints, photographs, and noise recorded by camera traps in the nest environment documented that herdsmen and farmers collected eggs. Rainfall coupled with strong winds also rolled eggs out of the nest and broke some of them. The main factors for nest failure were predation (52.39%, including hunting) followed by farming operations (19.05%) and desertion (9.52%) (Table 4). Potential predators commonly observed on the study sites were White-tailed Mongoose (Fig. 4C), Common Genets *Genetta genetta* and Fan-tailed Ravens *Corvus rhipidurus*.

Table 1. Geometrical egg parameters in three habitat types in UBNB (*N* = 224 eggs). Values are given as Mean ± SD for the whole data set (habitats combined) and separately per habitat. The same superscript letter within a row indicates a non-significant difference. Abbreviations: CTW = Combretum-Terminalia woodland and wooded grasslands; DAF = Dry evergreen Afromontane forest and grassland complex.

Geometric parameter	Habitats combined	Habitat			*H*	*P*
		CTW = 55	DAF = 25	Farmland = 144		
Length (mm)	42.13 (± 0.86; 40.02–43.70)	41.63 ± 0.88[b]	42.44 ± 0.71[a]	42.26 ± 0.81[a]	23.38	<0.001
Breadth (mm)	32.95 (± 0.73; 30.98–34.85)	32.62 ± 0.73[b]	32.95 ± 1.00[ab]	33.08 ± 0.63[a]	12.74	0.002
Mass (g)	25.20 (± 1.74; 21.29–28.76)	23.94 ± 1.56[b]	25.95 ± 1.18[a]	25.55 ± 1.66[a]	40.85	<0.001
Volume (cm³)	23.51 (± 1.31; 20.12–26.65)	22.76 ± 1.23[b]	23.69 ± 1.63[a]	23.77 ± 1.17[a]	21.87	<0.001
Surface area (cm²)	34.12 (± 1.23; 31.04–36.88)	33.37 ± 1.16[b]	34.36 ± 1.39[a]	34.36 ± 1.11[a]	24.43	<0.001
Shape index (%)	78.25 (± 1.79; 73.41–82.74)	78.37 ± 2.06[a]	77.64 ± 2.23[a]	78.31 ± 1.57[a]	0.78	0.677

Table 2. Spatiotemporal variation of clutch size. Abbreviations: AH - Afrotropical Highlands biome; SG - Sudan-Guinea Savanna biome. * Mann–Whitney test *U* = 443.5 and *P* < 0.001.

Category	Subcategory	2	3	4	5	6	7	N	Total	Mean ± SD	H	P
Habitat	CTW	0	14	8	5	2	0	29	111	3.83 ± 0.97[b]	13.95	0.001
	DAF	0	1	1	3	2	0	7	34	4.86 ± 1.07[ab]		
	Farmland	1	4	19	19	11	2	56	265	4.73 ± 1.04[a]		
Biome*	AH	0	9	17	23	14	2	65	308	5.14 ± 0.90[a]	NA	NA
	SG	1	10	11	4	1	0	27	102	3.78 ± 0.89[b]		
Month	September	0	3	5	4	4	0	16	73	4.56 ± 1.09[ab]	12.99	0.003
	October	0	5	12	16	10	2	45	216	4.80 ± 1.04[a]		
	November	1	6	9	3	2	0	21	83	3.95 ± 1.02[b]		
	December	0	5	3	3	0	0	11	38	3.82 ± 0.87[b]		

Clutch size (column group header over columns 2–7)

Table 3. Breeding parameters for measured and unmeasured nests of Harwood's Spurfowl.

Parameter	Measured nests			Unmeasured nests		
	Mean	SD	N	Mean	SD	N
Clutch size	4.46	1.09	92	5.48	0.80	27
Hatching success	4.12	0.91	57	5.22	0.80	23
Daily nest survival rates (DSR) (%)	98.82	0.003	78	99.45	0.003	27
Total nest survival probability (Ŝ) (%)	70.48	0.01	36	84.14	0.01	23

vegetation. In support of this, motionlessness is known to reinforce anti-predator coloration in many animal species (Stevens and Merilaita 2011, Stevens and Ruxton 2019), particularly among ground-nesting birds (Troscianko et al. 2016).

2. The location of most nests in terms of orientation, positioning, substrate, and slope gradient (accessibility) was apparently chosen to thwart unfavorable exposure to weather and to minimize the risk of predation. Consistent with these findings, ground nesters are known to employ such mechanisms to maintain a favorable thermal environment (Deeming and Mainwaring 2015, Mainwaring et al. 2015, Duursma et al. 2018) thereby optimizing nest safety (Gill 2007). Most Harwood's Spurfowls' nests were effectively hidden in vegetation, and some were located under single short thorny trees (up to 5 m) on steep slopes. This strategy minimized nest predation as suggested by Conover (2007) and Mainwaring et al. (2014).

3. Female Harwood's Spurfowls possibly also reduced the risk of depositional odor trails during feeding. Our camera trap recordings showed that incubating females never flew off directly from their nests and mainly left the nest in the morning. Instead, they typically walked away from the nests in different directions. Besides, we did not see individuals leaving the nest during rain and intensive solar radiation. Such behavior could, together with reducing visual encounters with predators, suggest that females minimize the risk of depositional odor trails in concordance with other reports on ground-dwelling birds (Conover 2007, Winkler 2016). For example, we had two failed nests due to olfactory-orientated predators, White-tailed Mongoose and Common Genet, who likely followed contact odor trails created by repeated visits, suggesting that breeding spurfowl females may be olfactory inconspicuous.

DISCUSSION

Mating system, nest-site selection, and nest-building behavior
We confirmed a polygamous, non-lekking mating system in Harwood's Spurfowl as previously reported (Robertson et al. 1997, Abrha et al. 2018). This is a resource-defense polygyny strategy (Emlen and Oring 1977, Gill 2007) typical of many galliform species (Lislevand et al. 2009, Winkler et al. 2015). Nest-site selection and nest-building behavior are critical for the breeding success of ground-nesting birds (Mayer et al. 2009, Mainwaring et al. 2014, Gömez et al. 2019). According to our results, only female Harwood's Spurfowls select nest sites. Their specific nest-site selection and nest-building behavior predominantly aims at reducing the risk of predation by the following mechanisms:

1. Plumage color and patterns of females often matched the background of the nest microhabitat (e.g., black soil, stones, rocks, and bushy thorns: Fig. 5; Append. 1). Such crypsis through background matching is a fundamental tactic of predator avoidance (Merilaita and Stevens 2011, Michalis et al. 2017, Ruxton et al. 2019, Terrill and Shultz 2023) and is very common in ground nesting birds (Lovell et al. 2013, Troscianko et al. 2016). In Ethiopia, some larks and other ground-breeding songbirds have evolved plumage traits to match different soil types (Last 2009). Based on our observations, incubating females remained motionless until being approached up to 1 m, suggesting that plumage crypsis plays the most important role for the survival of clutches because the lightly colored eggs are relatively conspicuous when unattended, even though the nests may be covered by

Table 4. Causes of breeding failure in Harwood's Spurfowls.

Successful nests (*N* = 57 nests)		Failed nests (*N* = 21 nests)			
Factor	Egg	Factor	Nest level	Laying parent	Total
Unhatched	18 (47.37%)	Predation	3 (14.29%)	1 (4.76%)	4 (19.05%)
Disappeared eggs	8 (21.05%)	Desertion	2 (9.52%)	-	2 (9.52%)
Egg collecting	9 (23.68%)	Hunting	8 (38.10%)	3 (14.29%)	11 (52.38%)
Sprawl/rolled eggs	3 (7.89%)	Farming	4 (19.05%)	0	4 (19.05%)
Total	38 (100%)	Total	17 (80.95%)	4 (19.05%)	21 (100%)

Egg laying, geometrical parameters of eggs, and clutch size
The onset of breeding was from the end of August, right after big rainfalls ceased, to December (in Ethiopia, this season is also known as "harvesting season" or "spring"). We found that Harwood's Spurfowl has a single breeding season instead of a prolonged or non-synchronous breeding as mentioned in Robertson et al. (1997). Such a difference in breeding phenology could be attributed to temporal changes of favorable habitats and climatic conditions, as well as differences in disturbance level. For example, the rainfall in the Upper Blue Nile Basin (UBNB) is highly variable but has trended toward significant decrease since 1980 (Mohammed et al. 2022). This could possibly influence the timing of breeding of the species. Indeed, the breeding season of Harwood's Spurfowl is associated with the rainy season (Robertson et al. 1997, Abrha et al. 2018) as in related species, such as Swainson's Spurfowl (*Pternistis swainsonii*) (Jansen and Crowe 2005) and most galliform species (McGowan 1994), probably due to food peaks after heavy and consecutive rainfall ceases.

Our results demonstrated that the earliest clutches were initiated in September, and peak egg laying occurred in October when the conditions were wet with occasional rainfall (Append. 4). Conversely, earlier studies reported the earliest egg-laying dates during the driest conditions in December and January (Ash 1978, Ash and Gullick 1989, Ash and Atkins 2009). However, these reports lacked systematic and detailed breeding observation of the target species in the area. According to our camera trap data (77.50%), many eggs were laid in the morning, which is consistent with other birds (Winkler 2016). The females laid on average a single egg per day, similar to other pheasants (Khalil et al. 2016) and other precocial species (Hepp and Kennamer 2018). Significant variation in the geometrical parameters of eggs across habitats could be explained by climatic conditions and food availability for females. The clutch size (4.66) for Harwood's Spurfowls was similar to that of Swainson's Spurfowl (Jansen and Crowe 2005). We found clutch size of Harwood's Spurfowl to decrease significantly as the breeding season progresses, possibly as a result of a gradual decline in food resources and nest cover, as well as an increase in threats (predominantly predation). This phenomenon is common in ground-nesting birds (Lu and Zheng 2003, Suárez et al. 2005, Balasubramaniam and Rotenberry 2016) because breeding females progressively face food scarcity (Winkler 2016).

Although linear egg dimensions of Harwood's Spurfowl were similar to its sister species, Clapperton's Spurfowl (*Pternistis clappertoni*) (Schönwetter 1961), we rely on the derived parameter (i.e., egg shape), as this parameter has an adaptive value for life-history traits in birds (Stoddard et al. 2017, Montgomerie et al. 2021). Moreover, egg shapes could be determined by clutch size (Barta and Székely 1997, Montgomerie et al. 2021). Following the classification of egg shape index (Sarica and Erensayin 2004, de Oliveira-Boreli et al. 2023), Harwood's Spurfowl has more spherical and whiter eggs, regardless of some phenotypic variation in shape, spottiness, and color across habitats (Appends. 2, 5). Because spherical egg shapes are characterized by a uniform shell thickness (Stoddard et al. 2017) and resistance to breakage (Bain 1991, Montgomerie et al. 2021), such traits (including egg color) in our study species could also represent an adaptation to excessive sunlight and erratic weather conditions in UBNB. For example, in Australian songbirds, the most spherical eggs were found among those species that bred in open nests under the hottest conditions, which exposed them to the highest amount of solar radiation (Duursma et al. 2018). We consider it possible that the spherical shape of Harwood's Spurfowls' eggs is a similar adaption to the harsh sunlight conditions in UBNB, which could also explain the spherical egg shape of other tropical galliform species (Stoddard et al. 2017, Montgomerie et al. 2021). To what extent the colors and patterns of Harwood's Spurfowls' eggs actually contribute to temperature regulation, which ultimately may account for enhanced breeding success, remains to be tested.

Incubation, hatching, and parental care
We found incubation to last for approximately 21 d, which matches the known incubation period of 21–23 d in other spurfowl species from South Africa (Little and Crowe 1993, Jansen et al. 2001). Although females sit on the nest after laying the first egg, incubation is delayed until the clutch is completed to guarantee hatching synchronicity. This is consistent with reports for many precocial birds, particularly ground nesters (e.g., Persson and Göransson 1999, Gill 2007, Mayer et al. 2009, Balasubramaniam and Rotenberry 2016, Winkler 2016). The average daily nest attendance of nearly 95% indicates that females actively reduce the risk of predation and egg hypothermia by leaving the nest only briefly for feeding. Our data thus documented that Harwood's Spurfowl has an almost uniparental care strategy, with females exclusively incubating the eggs and guiding their freshly hatched chicks to the nearby vegetation. The role of territorial males was mainly to escort the nesting females. Only in rare cases were males observed tossing food toward chicks. This indicates that males predominantly control the resources for the breeding females and by doing so, participate at least indirectly in raising their chicks. This is in accordance with the hitherto reported uniparental strategy in the congeneric Swainson's Spurfowl *Pternistis swainsonii* from South Africa (van Niekerk 2017) and other polygynous phasianids (Winkler et al. 2015).

Breeding success and failure

The average hatching success (86.94% at measured and 95.47% at unmeasured nests) of Harwood's Spurfowl is similar to some African (Gray-winged Francolin *Scleroptila afra*: Little and Crowe 1993; Red-winged Francolin *Scleroptila l. levaillantii*: Jansen et al. 2001) and Asian francolin species (Black Francolin *Francolinus francolinus asiae*: Kumar et al. 2020), but higher than reported for the other Gray Francolin (*Ortygornis pondicerianus interpositus*: Khalil et al. 2016). Even though we cautiously removed the vegetation cover and fenced trails leading to nests, we suspected that disturbances during repeated visits (e.g., camera placement, nest measurements, egg handling) could have exacerbated the failure of measured nests indirectly. Indeed, breeding success of measured nests was lower than that of unmeasured (random) nests, mainly due to predation and farming activities (Table 4). The relatively high percentage (47.37%) of unhatched eggs in successful nests could be due to infertility and embryo mortality. Touching eggs and catching laying parents in particular (Radnezhad et al. 2011, Zhao et al. 2020), as well as nest visits in general were reported as factors for hatching failure in other birds (Green 2004, Zhao et al. 2020). Because Harwood's Spurfowl is a ground nester mainly in and around farmlands, it is pronouncedly hunted for food (Robertson et al. 1997, Ash and Atkins 2009, Abrha and Nigus 2017, Abrha et al. 2017, 2023). Farming operations also exacerbated hatching failure of the species, consistent with studies in other pheasant species (Coates et al. 2017). Globally, predation is a major important threat for several galliform species (e.g., Little and Crowe 1993, Clark et al. 1999, Persson and Göransson 1999, Lu and Zheng 2003, Balasubramaniam and Rotenberry 2016, Zhao et al. 2020).

To conclude, as predation was the main reason for the nesting failure, we recommend limiting mowing grasses and cutting trees during the breeding season in and around farmlands and other habitats (including woodlands, scrub, and bush vegetation) where Harwood's Spurfowls are dwelling in order to avoid disturbance, sun exposure, and access to nesting sites. Hunting (including egg collecting) should be prohibited throughout the year, and conservation education and awareness creation should be delivered to the local communities.

Author Contributions:

Abadi Mehari Abrha: Conceptualization, data collection, data analysis, writing and revising paper Kai Gedeon: Conceptualization, funding acquisition, supervision, revising paper Lars Podsiadlowski: Conceptualization, funding acquisition, supervision, revising paper Till Töpfer: Conceptualization, data analysis, funding acquisition, supervision, writing and revising paper

Data Availability:

Data will be made available on request.

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Append. 1. Camera placement adjacent to nest location (A). A typical rock-dependent nest (B) and a nest under a short *Vachellia tortilis* tree (C and D) show background matching (plumage color and patterns of females and nesting sites) in Upper Blue Nile Basin (UBNB).

Append. 2. Variability in Harwood's Spurfowl egg colors and texture. Egg colors were white (A) and dusty white (B) with tiny spots in both nests. The clutch for (A) was taken out of the nest for handling and photography.

Append. 3. Pearson correlation coefficients for the geometrical egg parameters of Harwood's Spurfowl. ** Implies very significant correlation between parameters (P < 0.001).

Parameters	Length	Breadth	Weight	Volume	Surface area	Shape index
Length	1					
Breadth	.431**	1				
Weight	.434**	.277**	1			
Volume	.704**	.944**	.376**	1		
Surface area	.821**	.869**	.413**	.983**	1	
Shape index	-.488**	.577**	-.124	.276**	.097	1
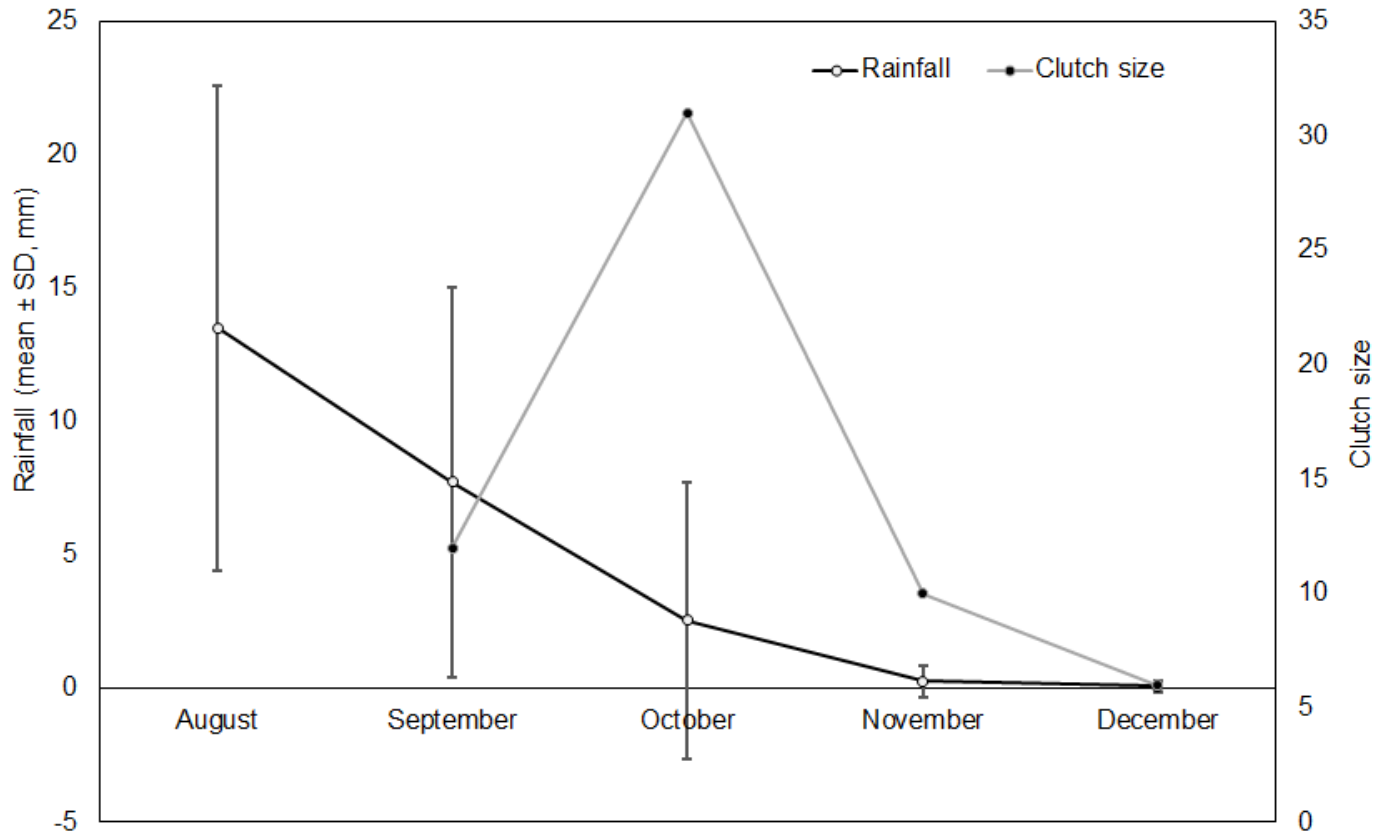
Append. 4. Average rainfall distribution and clutch size initiation in each month during the study period. Rainfall data was extracted from NASA/POWER satellite-based weather system (https://power.larc.nasa.gov/data-access-viewer/).

Append. 5. Variability in Harwood's Spurfowl egg shapes. Egg shapes ranged from oval to more spherical. The photographs depict both intra- and inter-clutch variation (A-D).