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Behavioural analysis of Village Weavers *Ploceus cucullatus* in an Ethiopian breeding colony during incubation: 1. Females

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We used video recordings to perform a behavioural analysis of a Village Weaver *Ploceus cucullatus* colony in Awash National Park, Ethiopia. We focused specifically on female behaviour during the pair-formation, egg-laying and early-incubation phases of the nesting cycle. A factor analysis revealed that females' temporal investments can be partitioned into three broad behavioural categories: (1) behaviours associated with aggression, (2) time away/inside nest, and (3) behaviours associated with copulation. Time budgets revealed females spent approximately 61% of their time away from the colony and 38% of their time inside their nests. The performance of individual behaviours was largely a function of temporal and social factors, including when the birds were observed and the personality of the territorial male. Females invested more time away from the nest earlier and more time inside the nest later in the observation period. One aspect of a territorial male's personality, boldness, was a predictor of several female behaviours: a female Village Weaver was significantly more likely to remain on a territory if the resident male had a tendency not to flee during colony-wide disturbances. Lastly, a path analysis revealed that females exhibited consistent sequential patterns of behaviour.

Analyse comportementale du Tisserin gendarme *Ploceus cucullatus* dans une colonie de reproduction éthiopienne pendant l'incubation: 1. Femelles

Nous avons utilisé des enregistrements vidéos pour effectuer une analyse comportementale d'une colonie du Tisserin gendarme *Ploceus cucullatus* dans le parc national d'Awash, en Éthiopie. Nous nous sommes concentrés sur le comportement des femelles pendant les phases de formation des couples, de ponte et d'incubation précoce du cycle de nidification. Une analyse factorielle a révélé que les investissements temporels des femelles peuvent être divisés en trois grandes catégories comportementales: (1) comportements associés à l'agression, (2) comportements à l'extérieur / à l'intérieur du nid et (3) comportements associés à la copulation. Les budgets-temps ont révélé que les femelles passaient environ 61% de leur temps loin de la colonie et 38% de leur temps dans leur nid. La performance des comportements individuels était largement fonction des facteurs temporels et sociaux, notamment le moment où les oiseaux étaient observés et de la personnalité du mâle territorial. Les femelles ont investi plus de temps loin du nid plus tôt au cours de la période d'observation et plus de temps à l'intérieur du nid plus tard. L'audace, l'un des aspects de la personnalité d'un mâle territorial, était un facteur prédictif de plusieurs comportements manifestés par les femelles: une femelle tisserin gendarme avait nettement plus de chances de rester sur un territoire si le mâle avait tendance à ne pas fuir lors de perturbations à l'échelle de la colonie. Enfin, une analyse de trajectoire a révélé que les femelles présentaient des modèles de comportement séquentiels cohérents.

Keywords: behaviour, Ploceidae, *Ploceus*, Village Weaver, weaverbirds

Introduction

The Village Weaver *Ploceus cucullatus* is a member of the Ploceidae, an Old World family comprised of 116 species in 17 genera (Craig 2010; Clements et al. 2017). The Village Weavers' distribution extends throughout sub-Saharan Africa (Craig 2010) with introduced populations found in islands in the Caribbean, the Indian Ocean and other localities (Lahti 2003; Dyer et al. 2017). Given their generalised diet, preference for human habitats and their ability to raise multiple broods per season, the Village Weaver is one of the most widespread and abundant of

the weaver species (Craig 2010). Their mating system is polygynous, as males vociferously compete with one another to establish territories, attract mates and to defend their nests within the larger colony. The colony itself can vary from fewer than 10 to hundreds of nests in a single tree (Collias and Collias 1969), and each male can build and defend multiple nests (Crook 1960). During the pair formation stage of the nesting cycle, an unmated female will enter a male's territory to inspect his nest. If a nest is repeatedly rejected, the male will tear it down and build a

fresh nest (Collias and Collias 1970, 1971a; Jacobs et al. 1978). If the female accepts the nest, she will line the interior with vegetation and form a pair bond with the male (Collias and Collias 1959, 1970, 1984). The repetition of pair-formation sequences – male display, female inspection, male singing and female lining of the nest – stimulates the ovaries of the female and subsequent sequences of copulation (Collias and Collias 1970). Following copulation, the female transitions into the egg-laying and incubation phases of the nesting cycle (Collias and Collias 1959, 1970, 1984). Here, we analyse the behavioural structure of female Village Weavers during these early phases of the nesting cycle: pair formation, egg-laying and early incubation.

The first comprehensive studies of Village Weaver behaviour during the breeding season were conducted approximately a half-century ago by the late ornithologists Elsie Collias, Nicholas Collias and John Hurrell Crook (Collias and Collias 1959; Crook 1963; Collias and Collias 1964, 1967, 1970, 1971a, 1971b). While these seminal studies provided comprehensive descriptive data on nest construction, territoriality, mating and parental behaviour, feeding and response to predation, they did not include detailed quantitative analyses of behavioural structure over a specified duration. Subsequent studies of female behaviour have mainly focused on experimental analyses of nest and mate selection (Collias and Victoria 1978; Jacobs et al. 1978; Collias et al. 1979); field surveys of eggs, nests and clutch size (Da Camara-Smeets 1982; Collias et al. 1986; Mgelwa et al. 2018); and responses to brood parasitism (Victoria 1972; Cruz and Wiley 1989; Robert and Sorci 1999; Lahti and Lahti 2002; Lahti 2005, 2006; Prather et al. 2007; Cruz et al. 2008). Strikingly, a large proportion of behavioural studies of Village Weavers have been male-centred and include analyses of male mating displays (Collias and Victoria 1978; Jacobs et al. 1978; Din 1992a), nest construction (Crook 1960; Collias and Collias 1962, 1964; Hall 1970; Collias and Collias 1973; Collias 1989; Din 1992a; Efenakpo et al. 2017), nest destruction (Hall 1970; Din 1992b), theft of nest materials (Din 1992b; Roulin 1999) and risk-taking behaviour (Habig and Lahti 2015; Habig et al. 2017). Hence, a detailed quantitative analysis of female behaviour during the breeding season is essential for understanding aspects of behavioural ecology specific to females.

The goal of this study was to provide a detailed quantitative analysis of female behaviour in a breeding Village Weaver colony in Awash National Park, Ethiopia during the pair-formation, egg-laying and early-incubation phases of the nesting cycle. To accomplish our goal, we analysed video of female behaviour, which allowed us to control for temporal and environmental differences and to observe a large repertoire of colonial behaviours simultaneously. Our study addressed three major questions:

(1) How do female Village Weavers partition their investment in time between different behaviours?
(2) Can we predict female behaviour based on: (i) time of day, (ii) date of observation, (iii) number of female nestmates, (iv) temperature or (v) territorial male behaviour?
(3) Do the behaviours of female Village Weavers follow consistent sequential patterns?

In the polygynous mating system of the Village Weaver, where reproductive variance is greater in males than females, we predict that females will almost exclusively invest in behaviours associated with parental effort during the early phases of the nesting cycle (Bateman 1948; Trivers 1972; Lee 2006).

Methods

We studied a Village Weaver breeding colony in Awash National Park, Ethiopia (8.85° N, 40.01° E) during July and August 2010. The peak of breeding in this species typically coincides with the rainy season (Da Camara-Smeets 1992), which at Awash spans from July to September (Abule et al. 2005). The colony was comprised of over 100 nests located in a fig tree (*Ficus* sp.) situated on the edge of the Awash River between the park and a sugar plantation. We identified focal females based on well-established behavioural cues: after a male constructs a nest, if a female accepts the nest, she will copulate with the resident male and line the interior of the nest with vegetation; she reliably returns to the same nest for the duration of the breeding cycle (Collias and Collias 1959, 1970, 1984). We also identified male territories based on all nests being clearly distinguished, and from a recognisable behavioural cue: after the construction of a nest, to attract mates, a male will perform an inverted wing-flapping display while hanging from his nest; this behaviour is only performed on their own nests (Crook 1963; Collias and Collias 1970, 1984). Based on these criteria, we identified 29 focal females each residing in one of 10 male territories.

We used a Canon VIXIA HF S21 camcorder to create high-definition (1 920 × 1 080 px) video recordings of the focal colony members on six different days over a two-week period. The colony was recorded for approximately 130 min d^{-1} and divided into roughly two, 65-min (66.9 ± 9.7 min) segments apportioned at different times each day such that by the end of the sixth day of recording, the entire 13 h duration spanning all daylight hours (between 06:30 and 19:30) was recorded with no time of day overlapping. During the recordings, the camera was placed in the same location daily (20 m from the colony) among littoral vegetation. The high-definition videos were studied in the laboratory using Adobe Premiere (Adobe Systems Inc., San Jose, CA, USA, 2009) in slow-motion allowing us to distinguish individual, hard-to-observe behaviours. For each observation, we selected one of the focal females and applied continuous sampling to manually code the frequency and duration of every behaviour observed (in seconds) throughout the 13 h time span. This process was repeated for all 29 females. During these observations, once focal females were observed lining their nests with vegetation, we could reliably infer that they were either in the egg-laying stage or early incubation stages (Collias and Collias 1959, 1970, 1984).

To better understand how female Village Weavers partition their investment in time between different behaviours, we used video observation to code 12 different behaviours using continuous sampling (Table 1). While performing these observations, we also completed 'field notes' in which we documented instances of unique

Table 1: Description of 12 behaviours performed by female Village Weavers during the observation period

Variable	Definition
Pecking a conspecific	Focal female strikes or bites another colony member using her beak
Physical contact with female	Focal female makes direct physical contact with another female without pecking
Inspecting nest	Focal female observes exterior and/or interior of nest by poking and pulling at materials
Pre-copulatory stance	Focal female raises tail slightly above horizontal position (Collias and Collias 1970)
Transporting vegetation	Focal female spends time away from territory, and when returning, is observed carrying plant material in her beak; female places the material into interior of the nest
Physical contact with male	Focal female makes direct physical contact with another male without copulation or pecking
Copulation	Focal female mates with a male
Hanging	Focal female suspends herself fully or partially outside the nest entrance
Flying	Focal female is moving through the air within colony
Perching	Focal female is alight or resting on a branch or twig within a male's territory
Inside nest	Focal female resides inside her nest
Time away	Focal female spends time away from territory

behavioural interactions that could not be described by simply coding the behaviour. Of the 12 behaviours that were coded, 10 behaviours were observed directly; two were inferred: (1) *time away* and (2) *transporting vegetation*. When a female left the breeding colony and returned with material to line the interior of her nest, we coded the entire duration of absence as transporting vegetation. If she returned without vegetation, we coded the entire duration of absence as time away. Transporting vegetation estimates could thus be overestimated (i.e. if females foraged while they were gathering nest materials). Given that total observation time varied between individuals, in order to compare durations between females, we calculated the weighted average of each individual behaviour by dividing the mean total observation time of all 29 females by the observation time of each individual; this allowed us to estimate the range and mean duration of time (in seconds) the colony females partitioned their behaviour during 13 h of observation (Table 2). For these data, we applied Pearson product-moment correlations to compare associations between individual behaviours.

We divided the data into 13 one-hour periods, and tested five predictors of female behaviour: (1) *time of day* (morning versus afternoon), (2) *date of observation* (given that the females were in the early stages of the nesting cycle synchronously, we were able to test whether female behaviour changed in earlier versus later observations), (3) *number of nestmates* (number of resident females residing on a male's territory), (4) *temperature* (temperature at onset of each observation period) and (5) *male fleeing probability* (probability a male would flee during a colony-wide disturbance). Briefly, a male was assigned a fleeing probability of 1 if he fled the colony during a disturbance and a score of 0 if he remained on the territory; these data were collected opportunistically during natural disturbances ($n = 36$ fleeing events; Habig et al. 2017). We modelled eight response variables: the probability (presence or absence) of (1) transporting vegetation, (2) physical contact with a male, and (3) copulation; the duration (in minutes) of (4) hanging, (5) flying, (6) perching, (7) time inside nest, and (8) time away (Table 1). To test the five predictors of female behaviour, we applied a generalised linear mixed model (GLMM) framework for measures of presence/absence data using binomial error distributions, and a linear mixed

Table 2: Range and mean duration of time (in seconds) that 29 colony females partitioned their behaviour during 13 h of observation of each female

Variable	Range	Mean	SD
Pecking a conspecific	0.0–0.1	0.003	0.019
Physical contact with female	0.0–0.6	0.02	0.1
Inspecting nest	0.0–2.8	0.2	0.6
Pre-copulatory stance	0.0–4.6	0.2	0.9
Transporting vegetation	0.0–444.1	32.2	88.2
Physical contact with male	0.0–21.1	1.5	4.1
Copulation	0.0–52.4	3.0	10.0
Hanging	0.0–376.3	64.7	95.8
Flying within territory	0.8–275.6	58.0	52.5
Perching	0.0–994.7	165.2	257.8
Inside nest	13.5–16 169.5	9 051.2	4 548.1
Time away	7 828.0–17 787.0	14 717.0	4 636.1

model (LMM) framework for duration data using Gaussian error distributions. Given that three response variables (hanging, flying and perching) were not normally distributed, we log-transformed (log + 0.5) these data; four behaviours (pre-copulatory stance, physical contact with a female, inspecting a nest and pecking a conspecific) were excluded from these analyses because they occurred infrequently. In addition, to reduce individual behaviours into a few interpretable underlying variables, we performed a factor analysis using the factanal function in R software (R Core Team 2018). For this analysis, we set the cutoff for loading at 0.4 and rotation at promax. By doing so, we were able to reduce the number of response variables into three discrete behavioural categories.
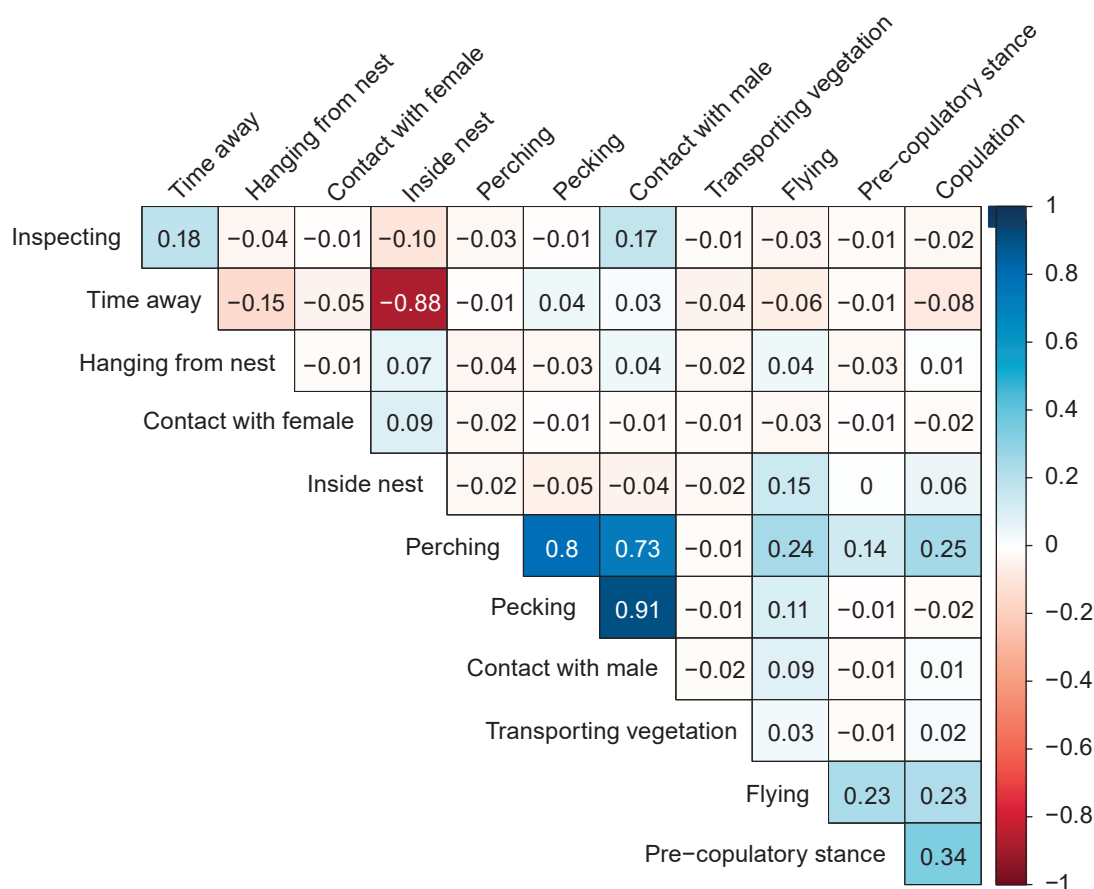
All GLMMs and LMMs were performed using the R packages lme4 (Bates et al. 2014) and lmerTest (Kuznetsova et al. 2015), and for each analysis, female identification was modelled as a random effect. To select the best fitting models, we used the drop1 function in the lme4 package (Bates et al. 2014), and confirmed the best fitting models using log likelihood ratio tests. Because one of the fixed effects of interest had missing data (male fleeing probability), we performed two sets of models. The first set, termed the 'main' models, tested predictors of individual female behaviour (and the three behavioural

categories) using all observations ($n = 173$). The predictors in these models included: time of day, date of observation, temperature and number of nestmates. The second set of models ($n = 125$), termed the 'subset' models, tested an additional predictor variable (male fleeing probability) where there were some missing data. Each subanalysis was run by testing whether the addition of male fleeing probability, using log likelihood ratio tests, significantly improved a model that included the best-supported fixed effects in the main model. If the addition of male fleeing probability did not improve model fit, then we present the results from the larger data set ($n = 173$). If the addition of male fleeing probability significantly improved model fit, then we present the model results using the reduced data set ($n = 125$).

Lastly, to test whether the behaviours of female Village Weavers follow consistent sequential patterns, we compiled the *frequency* of individual female behaviours using JWatcher 1.0 software (Blumstein 2010). The JWatcher software was used to perform path analyses, which included the calculation of *proportional incidence* (how frequently a behaviour occurred in a sequence relative to all other behaviours in the sequence) and *transitional probability* (the probability that one behaviour follows another sequentially). These data were the basis on which we created an ethogram representative of female behaviour (Blumstein and Daniel 2007; Blumstein 2010).

Results

We observed 29 focal females performing 12 different behaviours during the observation period (Table 1). Females spent most of their time either away from the colony ($61.1\% \pm 19.1\%$) or inside the nest ($37.6\% \pm 18.8\%$). The mean nesting bout length was 3.41 min (SD = 1.60), and the average off-bout was 3.69 min (SD = 1.18). Pairwise comparisons of time spent performing specific behaviours revealed several significant correlations (Table 2, Figure 1). The inspection of a male's nest by a female, a behaviour associated with female mate choice, was weakly, yet significantly correlated with both time away ($r = 0.18$, $p = 0.02$) and physical contact with a male ($r = 0.17$, $p = 0.02$). There was a strong correlation between female pecking of a conspecific, a behaviour associated with aggression, with both perching ($r = 0.80$, $p < 0.001$) and physical contact with a male ($r = 0.91$, $p < 0.001$). Likewise, physical contact with a male was positively and strongly correlated with perching within the male's territory ($r = 0.73$, $p < 0.001$). Two individual behaviours associated with reproduction were moderately correlated: copulation was positively associated with female performance of a pre-copulatory stance ($r = 0.34$, $p < 0.001$). There was also a moderate correlation between perching and copulation ($r = 0.25$, $p = 0.001$), flying within a colony and both the

Figure 1: Pairwise correlation coefficients of female behaviours performed by female Village Weavers in a breeding colony. Strong positive correlations are shown in dark blue; strong negative correlations are shown in dark red; moderate to weak positive correlations are indicated by light blue; moderate to weak negative correlations are indicated by pink

performance of a pre-copulatory stance ($r = 0.23$, $p = 0.002$) and copulation ($r = 0.23$, $p = 0.003$). Lastly, there was a strong negative correlation between time away from the colony and time spent inside the nest ($r = -0.88$, $p < 0.001$).

The performance of individual behaviours by females was largely predicted by date of observation (earlier or later in the observation period) and male fleeing probability, to a lesser extent by time of day (AM or PM) and, to even a lesser extent, by number of nestmates and temperature (Table 3). Females were more likely to spend time away from the colony (estimate: -2.61, $p < 0.001$), engage in physical contact with a male (estimate: -0.33, $p = 0.006$) and perch in a male's territory (estimate: -0.14, $p = 0.003$) earlier than later in the observation period. Later in the observation period, a female was more likely to be inside her nest (estimate: 2.49, $p < 0.001$). For three behaviours, the addition of male fleeing as a fixed effect significantly improved model fit (Table 3): A female was more likely to fly within the colony (estimate: -0.88, $p = 0.003$), perch within a male's territory (estimate: -0.13, $p = 0.03$) and remain inside her nest (estimate: -17.52, $p = 0.03$) if the territorial male remained on his territory rather than fleeing during colony wide disturbances. Females were more likely to copulate with a male in the morning than in the afternoon (estimate: -1.76, $p = 0.046$) and hang from their nests during warmer temperatures (estimate: 0.05, $p = 0.002$). Lastly, the number of nestmates was a significant predictor of time away from the colony: a female was more likely to spend time away from the colony if she resided on a territory with a male who had more resident females than on a territory with a male who had fewer resident females (estimate: 8.31, $p = 0.006$).
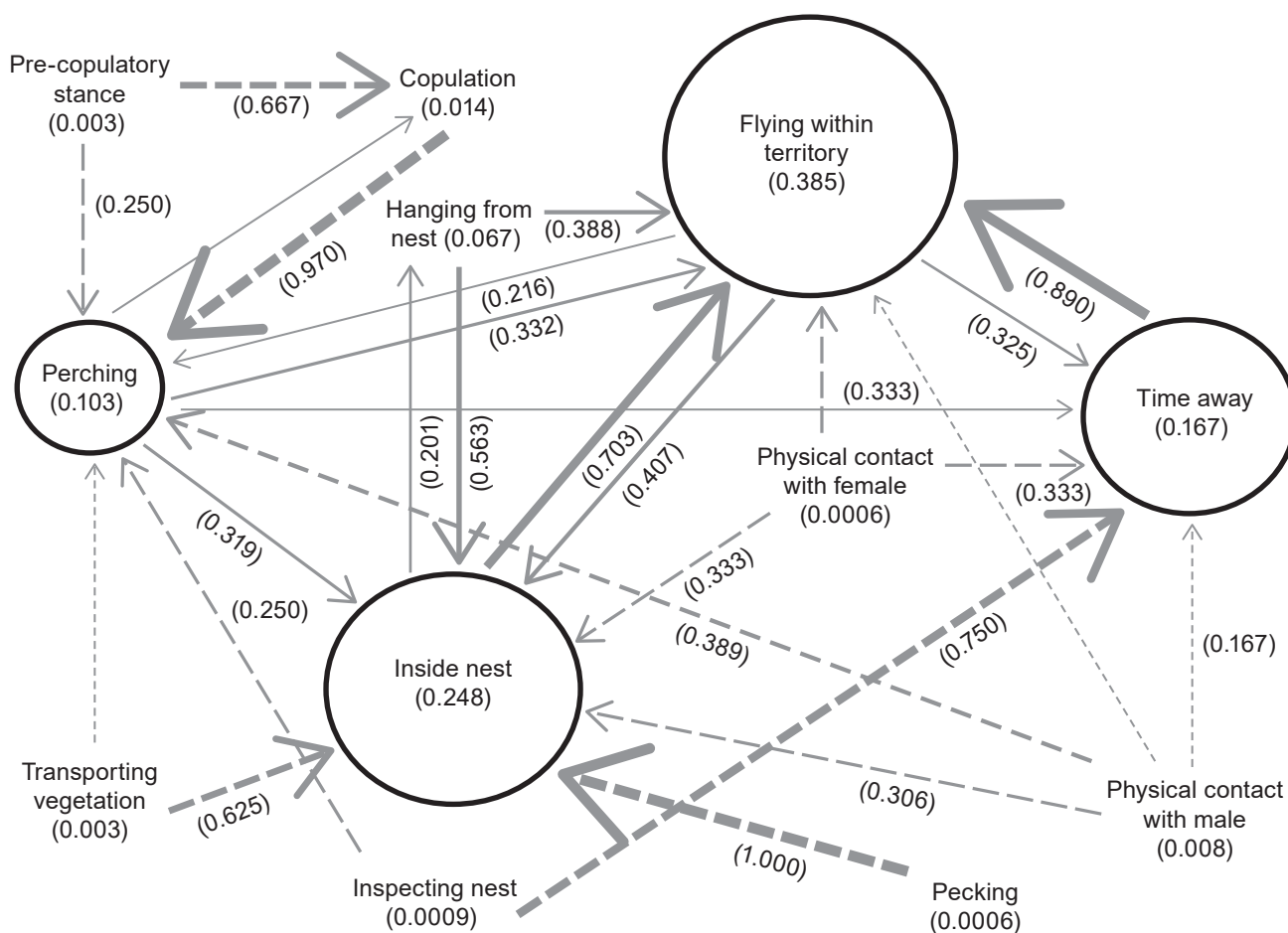
A factor analysis reduced the data set into three summary variables. Factor 1 explained 21.0% of the variance, and reflects a high incidence of behaviours associated with aggression (pecking, physical contact with a male and perching in a male's territory). Factor 2 explained 15.0% of the variance representing a negative correlation between time away and time inside nest. Factor 3 explained 8.0% of the variance, reflecting behaviours associated with copulation (copulation and pre-copulatory stance). Based on the three summary variables identified by the factor analysis, we found that females allocated almost all of their time either inside the nest or away from the colony (Factor 2: $98.7\% \pm 1.3\%$); the remainder of their time was partitioned between behaviours associated with aggression (Factor 1: $0.70\% \pm 1.1\%$) and behaviours associated with copulation (Factor 3: $0.30\% \pm 0.04\%$). The performance of the three composite behaviours was associated with different predictors: (1) behaviours associated with Factor 1 (pecking, physical contact with a male and perching) tended to take place in the morning than in the afternoon (estimate: -0.42, SE $= 0.24$, $t = -1.74$, $p = 0.08$, $n = 173$); (2) behaviours associated with Factor 2 (time away/inside nest) were more likely to occur during the afternoon than in the morning (estimate: 23.85, SE $= 2.62$, $t = 9.12$, $p < 0.001$, $n = 173$), during cooler rather than warmer temperatures (estimate: -2.01, SE $= 0.25$, $t = 8.14$, $p < 0.001$, $n = 173$), and on a territory in which the focal female had more rather than fewer nestmates (estimate: 3.50, SE $= 0.90$, $t = 3.88$, $p < 0.001$, $n = 173$); (3) behaviours associated with Factor 3

Table 3: Best-supported models of predictors of individual behaviours of female weavers. Sample sizes for transporting vegetation, physical contact with male, hanging from nest and time away are based on the main model (29 females and 173 observation hours). The following predictor variables were included in the main model: time of observation (AM or PM), day of observation (earlier or later in the nesting cycle), number of nestmates and temperature. Sample sizes for copulation, flying, perching and inside nest are based on the subset model (reduced data set of 29 females and 125 observation hours that included 36 fleeing events). The following predictor variables were included in the subset model: time of observation (AM or PM), day of observation (earlier or later in the nesting cycle), number of nestmates, temperature and male fleeing probability. The best-supported models (shown below) were selected based on log likelihood ratio tests

Fixed effects	Estimate	SE	t-value	P
Response variable: transporting vegetation to line nest				
Time of day (PM)	-1.33	0.83	-1.60	0.110
Response variable: physical contact with male				
Day of observation	-0.33	0.12	-2.73	0.006
Response variable: copulation				
Time of day (PM)	-1.76	0.88	-1.99	0.046
Day of observation	-0.53	0.27	-1.98	0.047
Response variable: hanging from nest				
Temperature	0.05	0.02	3.11	0.002
Response variable: flying in male's territory				
Day of observation	-0.07	0.02	-2.93	0.004
Male fleeing	-0.83	0.28	-3.02	0.003
Response variable: perching in male's territory				
Day of observation	-0.14	0.05	-3.00	0.003
Male fleeing	-0.13	0.52	-2.19	0.030
Response variable: time away				
Number of nestmates	8.31	2.97	2.80	0.006
Day of observation	-2.61	0.73	-3.55	<0.001
Response variable: inside nest				
Day of observation	2.49	0.69	3.61	<0.001
Male fleeing	-17.52	7.88	-2.22	0.029

(copulation, pre-copulatory stance) were more likely to take place earlier rather than later in the observation period (estimate: -0.08, SE $= 0.03$, $t = -2.55$, $p = 0.01$, $n = 173$). Lastly, we found that the addition of male fleeing probability as a fixed effect did not significantly improved model fit for all three composite behaviours.

A path analysis revealed moderate to strong tendencies across individuals in behavioural sequences of females (Figure 2). We recorded 4 638 sequential behaviours; the four most common were flying (38.5%), inside nest (24.8%), time away (16.7%) and perching (10.3%). These four behaviours exhibited a wide range of transitional probabilities. If a female was observed flying in the colony, her transition probability of residing inside the nest was 0.41 ($z = 19.87$, $p < 0.001$), time away 0.33 ($z = 22.83$, $p < 0.001$) and perching 0.22 ($z = 19.99$, $p < 0.001$). Following time away and inside nest, the transitional probabilities of a female flying in the colony were 0.89 for time away and 0.70 for inside nest (time away: $z = 25.57$, $p < 0.001$; inside nest: $z = 31.62$, $p < 0.001$) and for inside nest only, the transitional probability that a female would next hang from her nest was 0.20 ($z = 21.17$, $p < 0.001$). Lastly, if a

Figure 2: Ethogram indicating the frequency of performance of behaviours and the proportional incidence of sequential acts, averaged across 29 female Village Weavers during 13 h of video analysis over 6 d. The diameter of each circle and the corresponding number represent the proportional frequency of performance of each behaviour. The thickness of each arrow indicates the transitional probability between two behaviours (the probability that one behaviour follows another sequentially). Transition probabilities over 0.15 are labelled; transition probabilities between 0.10 and 0.15 are represented by unlabelled arrows; transition probabilities less than 0.10 are not shown. Transitions from behaviours with proportional frequencies <0.05 are represented by dashed lines because probabilities are less reliable

female was observed perching within a male's territory, the transition probability of flying within a male's territory was 0.33 ($z = -2.52$, $p = 0.012$), residing inside the nest 0.32 ($z = 3.82$, $p < 0.001$), and copulation 0.12 ($z = 20.44$, $p < 0.001$).

Three examples of rare female behaviours were recorded during the observation period. First, on three separate occasions, individual females were observed inspecting and then temporarily residing in nests that were not fully constructed by the territorial male. In all three of these cases, each female eventually rejected the 'skeletal' nest and each male returned to constructing these nests to completion. In one of these three cases, the female inspected the unfinished nest, resided in the nest repeatedly, until she eventually rejected the nest. On subsequent days, females eventually accepted each of these nests upon completion. The second rare behaviour that we observed occurred when one female approached a male's territory and perched on a branch near his newly constructed nest. A female residing in a neighbouring male's territory entered this adjacent territory and began

fighting with the visiting female. The territorial male from this adjacent territory intervened, displacing the visiting female while the female that was residing on his territory returned to her nest. Lastly, we observed one case in which a female attempted to enter a nest that had been occupied by another female for an extended period. The presumed resident female repeatedly pecked the interloper, who flew away but then attempted to enter the occupied nest a second time. The resident female again pecked the intruding female until the interloper gave up and flew away.

Discussion

In our observational study of a breeding colony of Village Weavers in Ethiopia, time budgets revealed that females' temporal investments focused almost exclusively on two behaviours: time away and time inside nest. In addition to these two dominant behaviours, individual females varied in their behavioural repertoires, which included an assortment of behaviours associated with the pair-formation, egg-laying and early-incubation phases of the nesting

cycle (Table 1). Differences in individual behaviours were largely influenced by temporal and social factors, including when the birds were observed and the personality of the territorial male. Furthermore, in accordance with Collias and Collias (1970), we found that female Village Weavers exhibited predictable sequential patterns of behaviour. Our results, particularly the time budgets of female weavers, are largely consistent with evolutionary theory, which predicts that in polygynous mating systems where reproductive variance is greater in males than females, females are expected to invest heavily in parental effort while males are expected to allocate energetic resources towards mate attraction and retention (Bateman 1948; Trivers 1972; Lee 2006). In support, females' temporal investments in this colony focused almost exclusively on behaviours typically associated with parental investment. In addition, in a parallel study of male Village Weavers of the same population (Khan et al. 2019), males allocated energetic resources towards overall mate attraction and retention, including the construction of multiple nests and the attraction and mate-guarding of multiple females. Moreover, in Village Weavers, the female alone incubates the eggs (Collias and Collias 1970; Collias and Victoria 1978; Khan et al. 2019).

Females partitioned their investment in time based on three broad categories: (1) behaviours associated with aggression, (2) time away/inside nest, and (3) behaviours associated with copulation. First, behaviours associated with aggression – pecking, physical contact with a male and perching in a male's territory – were all positively correlated. This relationship was borne out by a factor analysis and explained 21.0% of the observed behavioural variation. Second, time away and time inside nest explained 15.0% of the behavioural variance according to a factor analysis. These behaviours were negatively correlated: females who spent more time away from the colony spent less time inside their nests, and vice versa. Our results were somewhat similar to a previous study of four female Village Weavers that took place over a 10 h period on a single day (Collias and Collias 1970). In this 1970 study, the average time a female spent away from her nest was 4.0 min; in the present study, the average off-bout duration for 29 focal females was 3.7 min. However, Collias and Collias (1970) found that the average time their four focal females spent in the nest and presumably on eggs was 6.1 min, which was higher than the 3.4 mins reported in our study. This discrepancy might be explained by differences in the number of days of observation between studies. Interestingly, we found that behavioural investment in time away and time inside nest changed over time: females invested more time away from the colony earlier than later and more time inside their nests later than earlier in the observation period. Lastly, in alignment with previous studies (Crook 1963; Collias and Collias 1970), behaviours associated with sequences of copulation – pre-copulatory stance and copulation – were positively correlated. According to a factor analysis, this relationship explained 8.0% of the observed behavioural variance.

Some aspects of female behaviour were largely predicted by time of day, temperature, and date of observation. First, in time of day analyses, copulation was more common in the morning than in the afternoon. Given that copulation is energetically costly, it might be more efficient for weavers to mate in the cooler morning than in the afternoon. In support, a review of copulation behaviour across several avian taxa found that most birds copulate during the morning hours (Birkhead et al. 1987). Second, in temperature analyses, we found that females spent more time hanging from their nests during warmer temperatures. This finding is consistent with the observation that female Village Weavers conserve energy by sitting steadily inside their nests during the cool night and early dawn (Collias and Collias 1967). Whether variation in movement behaviour, in terms of whether a female sits steadily inside her nest or suspends herself fully or partially outside the nest entrance, is driven by differences in temperature remains untested. Lastly, in our date of observation analyses, five individual behaviours – perching within a male's territory, flying within the colony, physical contact with a male, copulation and time away – were more likely to occur earlier than later in the observation period, whereas only one individual behaviour – residing inside the nest – was more likely to occur later than earlier in the observation period. Given that the nesting cycle follows a sequential pattern of behaviours – copulation followed by egg-laying and egg-laying followed by incubation – our findings were consistent with the breeding biology of Village Weavers (Collias and Collias 1970); that is, females engage in behaviours associated with mating effort (e.g. copulation) and nutrient procurement (e.g. foraging) more frequently prior to the egg-laying and incubation phases of the breeding cycle, and behaviours associated with reproduction (e.g. remaining in the nest) more frequently during the egg-laying and incubation phases of the breeding cycle. Indeed, this was the pattern observed in our quantitative analyses.

Female behaviour was associated with two social factors: number of nestmates and male fleeing probability. In terms of number of nestmates, females residing on territories with more females spent significantly more time away from the colony than females residing on territories with fewer females. This finding suggests that females have reduced opportunities to leave the colony in situations in which the territorial male has fewer females to mate guard. In support, male Village Weavers are known to chase females when they attempt to exit their nests (Collias and Collias 1970). However, compared with closely related species, male Village Weavers have stronger nest attachment and tend not to stray too far from their territory (Crook 1963). A second social factor, male fleeing probability, was a significant predictor of several female behaviours. Specifically, a female Village Weaver was significantly more likely to remain on the male's territory (i.e. flying, perching and residing inside the nest) if the territorial male had a tendency *not* to flee during colony-wide disturbances. In fact, Village Weaver males have been found to be greater risk-takers – they are less likely to flee and return to the nest sooner if they do flee – as the number of mates increase (Habig et al. 2017). Thus, our results suggest that females tend to leave when they can (i.e. when nobody's watching), but they are also more likely to stay when the resident male exhibits a bold personality (i.e. the resident male tends not to flee during colony-wide disturbances).

Finally, we were interested in determining whether female Village Weavers exhibited consistent sequential patterns of behaviour. While our time budget analyses revealed that time away and time inside nest were the most dominant behaviours in terms of duration, in our sequential analyses, the four most frequently observed behaviours (in descending order) were: flying within a male's territory, inside nest, time away and perching. These four behaviours were either preceded or followed by behaviours exhibiting high transition probabilities. Both perching and flying within a male's territory, for instance, were consistent precursors to time inside nest and time away. Likewise, the temporal sequence of flying within a male's territory, followed by perching within a male's territory, were both precursors to copulation. These findings quantitatively confirm copulatory sequences described by Crook (1963) and Collias and Collias (1970) during behavioural observations of Village Weavers in West Africa. Thus, consistent with our analyses of time budgets and descriptive studies of sequential behaviour (e.g. Crook 1963; Collias and Collias 1970), our results suggest that these sequential patterns appear to represent functional suites of behaviour.

Building on previous studies, many of which were completed almost a half-century ago (e.g. Collias and Collias 1959, 1964, 1967, 1970, 1971a, 1971b; Crook 1963), our detailed analyses of the behavioural ecology of female Village Weavers afforded us the opportunity to ask new questions and to perform additional analyses. Our quantitative analyses of time budgets, predictors of behaviour and temporal sequences allowed us to map the structure and sequence of female behaviour during the pair-formation, egg-laying and early-incubation phases of the nesting cycle. In support of evolutionary theory (Trivers 1972; Lee 2006), our results provide support for the idea that females in polygynous societies allocate energetic investments towards behaviours that maximise parental investment. We consider that future quantitative studies, extended over longer periods to include the late incubation and nestling phases of the breeding cycle, will help us to further understand the behavioural ecology and energetic investments of female Village Weavers.

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References

Abule E, Smit GN, Snyman HA. 2005. The influence of woody plants and livestock grazing on grass species composition, yield and soil nutrients in the Middle Awash Valley of Ethiopia. *Journal of Arid Environments* 60: 343–358.

Bateman AJ. 1948. Intra-sexual selection in *Drosophila*. *Heredity* 2: 349–368.

Bates D, Mächler M, Bolker B, Walker S. 2014. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67: 1–48.

Birkhead TR, Atkin L, Møller AP. 1987. Copulation behaviour of birds. *Behaviour* 101: 101–138.

Blumstein DT. 2010. JWatcher version 1.0. Available at http://www.jwatcher.ucla.edu/.

Blumstein DT, Daniel JC. 2007. *Quantifying behaviour the JWatcher way*. Sunderland, MA: Sinauer Associates.

Clements JF, Schulenberg TS, Iliff MJ, Roberson D, Fredericks TA, Sullivan BL, Wood CL. 2017. The eBird/Clements checklist of birds of the world: v2016. Available at http://www.birds.cornell.edu/clementschecklist/download/ [accessed 14 January 2019].

Collias EC, Collias NE, Jacobs CH, Cox CR, McAlary FA. 1986. Old age and breeding behaviour in a tropical passerine bird *Ploceus cucullatus* under controlled conditions. *The Auk* 103: 408–419.

Collias EC, Collias NE, Jacobs CH, McAlary F, Fujimoto JT. 1979. Experimental evidence for facilitation of pair formation by bright color in weaverbirds. *The Condor* 81: 91–93.

Collias NE. 1989. The principle of self-reinforcement in nest building: evidence from abnormal nests of a weaverbird (*Ploceus cucullatus*). *Etología: Revista de la Sociedad Española de Etología* 1: 87–96.

Collias NE, Collias EC. 1959. Breeding behaviour of the Black-headed Weaverbird *Textor cucullatus graueri* (Hartert) in the Belgian Congo. *Ostrich* 30: 233–241.

Collias NE, Collias EC. 1962. An experimental study of the mechanisms of nest building in a weaverbird. *The Auk* 79: 568–595.

Collias NE, Collias EC. 1964. The development of nest-building behaviour in a weaverbird. *The Auk* 81: 42–52.

Collias NE, Collias EC. 1967. A quantitative analysis of breeding behaviour in the African Village Weaverbird. *The Auk* 84: 396–411.

Collias NE, Collias EC. 1969. Size of breeding colony related to attraction of mates in a tropical passerine bird. *Ecology* 50: 481–488.

Collias NE, Collias EC. 1970. The behaviour of the West African Village Weaverbird. *Ibis* 112: 457–480.

Collias NE, Collias EC. 1971a. Comparative behaviour of West African and South African subspecies of *Ploceus cucullatus*. *Ostrich* 42: 41–52.

Collias NE, Collias EC. 1971b. Some observations on behavioural energetics in the Village Weaverbird. I. Comparison of colonies from two subspecies in nature. *The Auk* 88: 124–133.

Collias NE, Collias EC. 1973. Further studies on development of nest-building behaviour in a weaverbird (*Ploceus cucullatus*). *Animal Behaviour* 21: 371–382.

Collias NE, Collias EC. 1984. *Nest building and bird behaviour*. Princeton: Princeton University Press.

Collias NE, Victoria JK. 1978. Nest and mate selection in the Village Weaverbird (*Ploceus cucullatus*). *Animal Behaviour* 26: 470–479.

Craig AJFK. 2010. Family Ploceidae (Weavers). In: del Hoyo J, Elliot A, Christie DA (eds), *Handbook of the birds of the world, vol. 15: Weavers to New World warblers*. Barcelona: Lynx Editions. pp 165–166.

Crook JH. 1960. Nest form and construction in certain West African weaver-birds. *Ibis* 102: 1–25.

Crook JH. 1963. Comparative studies on the reproductive behaviour of two closely related weaver bird species (*Ploceus cucullatus* and *Ploceus nigerrimus*) and their races. *Behaviour* 21: 177–231.

Cruz A, Prather JW, Wiley JW, Weaver PF. 2008. Egg rejection behaviour in a population exposed to parasitism: Village Weavers on Hispaniola. *Behavioral Ecology* 19: 398–403.

Cruz A, Wiley JW. 1989. The decline of an adaptation in the absence of a presumed selection pressure. *Evolution* 43: 55–62.

Da Camara-Smeets M. 1982. Nesting of the Village Weaver *Ploceus cucullatus*. *Ibis* 124: 241–251.

Din NA. 1992a. Breeding of the Black-headed Village Weaver (*Ploceus cucullatus*) and the Chestnut-and-black Weaver (*P. nigerrimus*) in Ile-Ife, Nigeria. *African Journal of Ecology* 30: 49–64.

Din NA. 1992b. Pattern of nest destruction in the two village weavers (*Ploceus cucullatus* and *P. nigerrimus*) at Ife, Nigeria. *African Journal of Ecology* 30: 261–268.

Dyer EE, Redding DW, Blackburn TM. 2017. The global avian invasions atlas, a database of alien bird distributions worldwide. *Scientific Data* 4: 170041.

Efenakpo OD, Ijeomah HM, Bunza MS. 2017. Preference of nesting material by Village Weaver birds (*Ploceus cucullatus*). *Journal of Research in Forestry, Wildlife and Environment* 9: 19–27.

Habig B, Chiyo PI, Lahti DC. 2017. Male risk-taking is related to number of mates in a polygynous bird. *Behavioral Ecology* 28: 541–548.

Habig B, Lahti DC. 2015. Heterospecific intrusions, synchronous fleeing, and nest attendance in a weaverbird colony. *Journal of Ornithology* 156: 551–555.

Hall JR. 1970. Synchrony and social stimulation in colonies of the Black-headed Weaver *Ploceus cucullatus* and Vieillot's Black Weaver *Melanopteryx nigerrimus*. *Ibis* 112: 93–104.

Jacobs CH, Collias NE, Fujimoto JT. 1978. Nest colour as a factor in nest selection by female Village Weaverbirds. *Animal Behaviour* 26: 463–469.

Khan K, Habig B, Lahti DC. 2019. Behavioural analysis of Village Weavers *Ploceus cucullatus* in an Ethiopian breeding colony during incubation: 2. Males. *Ostrich*. DOI: 10.2989/00306525.2019.1616231.

Kuznetsova A, Brockhoff P.B, Christensen BRH. 2015. Package 'lmerTest': tests in linear mixed effects models. R package version 2.0. Available at https://cran.r-project.org/web/packages/lmerTest/lmerTest.pdf.

Lahti DC. 2003. A case study of species assessment in invasion biology: the Village Weaverbird *Ploceus cucullatus*. *Animal Biodiversity and Conservation* 26: 45–55.

Lahti DC. 2005. Evolution of bird eggs in the absence of cuckoo parasitism. *Proceedings of the National Academy of Sciences of the USA* 102: 18057–18062.

Lahti DC. 2006. Persistence of egg recognition in the absence of cuckoo brood parasitism: pattern and mechanism. *Evolution* 60: 157–168.

Lahti DC, Lahti AR. 2002. How precise is egg discrimination in weaverbirds? *Animal Behaviour* 63: 1135–1142.

Lee KA. 2006. Linking immune defenses and life history at the levels of the individual and the species *Integrative and Comparative Biology* 46: 1000–1015.

Mgelwa AS, Abrha AM, Kabalika Z, Tamungang SA, Nigusse AGM. 2018. Habitat utilisation and nesting behaviour of two sympatric weavers in Mbalmayo District, Cameroon. *Ostrich* 89: 163–172.

Prather JW, Cruz A, Weaver PF, Wiley JW. 2007. Effects of experimental egg composition on rejection by Village Weavers (*Ploceus cucullatus*). *Wilson Journal of Ornithology* 119: 703–711.

Robert M, Sorci G. 1999. Rapid increase of host defence against brood parasites in a recently parasitized area: the case of Village Weavers in Hispaniola. *Proceedings of the Royal Society B: Biological Sciences* 266: 941–946.

R Core Team 2018. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing.

Roulin A. 1999. Stealing of nest material in *Ploceus cucullatus nigriceps*: costs and benefits of coloniality. *Ostrich* 70: 152.

Trivers RL. 1972. Parental investment and sexual selection. In: Campbell B (ed.), *Sexual selection and the descent of man, 1871–1971*. Chicago: Aldine Publishing Co. pp 137–179.

Victoria JK. 1972. Clutch characteristics and egg discriminative ability of the African Village Weaverbird *Ploceus cucullatus*. *Ibis* 114: 367–376.