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Behavioural analysis of Village Weavers *Ploceus cucullatus* in an Ethiopian breeding colony during early incubation: 2. Males

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We observed a colony of Village Weavers *Ploceus cucullatus* in Ethiopia at the height of the breeding season to assess variation and relationships amongst male behaviours. Individuals spent most of their time on behaviours functioning in acquiring and retaining mates, and invested more time in female choice (i.e. nestbuilding and display) compared with male competition (i.e. territory defence and stealing nest material). Males exhibited a tradeoff between competing with other males and attending to or building nests. Stealing nest materials functioned as sabotage rather than for nestbuilding. Tradeoffs were also evident between interacting with females and both constructing nests and leaving the colony to forage. Males left the colony frequently, but only stayed away long when gathering nest materials. As individual males acquired more mates, they visited their nests more often but shifted away from building nests and towards defending them. Individuals differed markedly in their behavioural patterns, but variation was continuous.

Analyse comportementale de Tisserin gendarme *Ploceus cullucatus* au sein d'une colonie de reproduction durant l'incubation précoce : 2. Males

Nous avons observé une colonie de Tisserin gendarme *Ploceus cucullatus* en Ethiopie au plus pic de la saison de reproduction pour évaluer les variations et relations parmi les comportements des mâles. Les individus passaient le plus clair de leur temps à adopter des comportements permettant d'acquérir et de retenir des partenaires et ont investi plus de temps dans le choix d'une femelle (p.ex construction de nid et parade) que dans la compétition avec d'autres males (p.ex défense territoriale and vol de matériau de nidification). Les males présentaient un compromis entre concurrencer d'autres males et assister aux nids ou les construire. Le vol de matériel de nidification s'apparentait plus à du sabotage qu'a de la construction. Des compromis étaient aussi évidents entre interagir avec les femelles et construire les nids plutôt que quitter la colonie en quête de nourriture. Les mâles quittaient la colonie fréquemment, mais ne demeuraient loin pour de longues périodes que pour rassembler des matériaux de nidifications. En tant qu'individus les mâles acquièrent plus de partenaires, ils visitent leurs nids plus souvent mais s'éloignent de la construction de nids pour se consacrer à leur défense. Les comportements différaient considérablement d'un individu à l'autre, mais la variation était continue.

Keywords: coloniality, ethogram, mating system, Ploceidae, *Ploceus*, sexual selection, weaverbirds

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Introduction

Village Weavers *Ploceus cucullatus* are colonially breeding, polygynous birds (Collias and Collias 1959, 1967). Males build multiple nests, and conspicuous male advertisement displays beneath these nests attract females to the colony (Hall 1970). Females choose mates based partly on the quality of nest construction (Collias and Victoria 1978; Jacobs et al. 1978). The area within which a male builds his nests he treats as a territory, defending it from other males even as he continues to build and attempts to attract mates (Collias and Collias 1959; Crook 1963; Din 1992). This situation creates a tension between sexually selected traits and survival-related traits (Andersson 1994), and between behaviours that aid in competition with rivals and those that aid in attracting mates (Wong and Candolin 2005; Hunt et al. 2009). The broader context for these interactions and tensions is an organism's overall behavioural structure, which has been captured for various species to some extent by time budgets and ethograms (Collias and Verbeek 1972; Ropert-Coudert et al. 2004). Assessing behavioural structure quantitatively and in real time can be challenging in birds because of their mobility and often rapid changes in behaviour. Village Weaver breeding colonies offer a valuable opportunity, because males perform a large proportion of their behaviours within the colony, and an entire colony or a portion of it can be video recorded for more careful analysis later. Although the behaviour of male Village Weavers has been subject to intensive investigation for over half a century (as referenced above and

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in Habig et al. 2019), none of these studies assessed comprehensive behavioural repertoires quantitatively for multiple individuals. Thus, a detailed analysis of behavioural structure over a specified duration would be informative.

In this study, we quantify male behaviour at a breeding colony of the Ethiopian Village Weaver *P. c. abyssinicus* Gmelin, 1789 during the early stage of the breeding cycle (laying and early incubation). As such, this study is a companion piece to Habig et al. (2019), which focuses on the behaviour of females in the same colony. We especially ask three questions, related to categories, variation and sequences of behaviour, respectively:

- How do male Village Weavers partition their time investment amongst different behaviours?
- Do males vary amongst each other in the way they allocate time to different behaviours, or shift their allocation depending on the number of mates they have acquired?
- Do the behaviours of male Village Weavers follow consistent sequential patterns?

Materials and methods

We recorded and subsequently observed high-definition video of a breeding colony of the Village Weaver in Awash National Park in Ethiopia (8.845° N, 40.006° E) over a six-day period during July and August 2010. The colony consisted of over 100 nests in a single tree (*Ficus* sp.) on the bank of the Awash River, between the park and a sugar plantation. We identified 10 males in the field, each of which had at least one nest in the egg-laying or incubation stages of breeding (having been chosen and lined by a female no more than 5 d before the onset of recording); we set the videorecorder's field of view so that the territories of all 10 of these males were visible. Throughout the period of recording, females spent significant time inside these nests, but did not carry food into them. Although we did not mark birds, male Village Weavers are known to remain with the nests they build and to defend them during incubation of the eggs and rearing of young; females reliably return to the nests they choose and attend to the eggs and young there (Collias and Collias 1959; Crook 1963; Collias and Collias 1970). Thus, we used nests as our means of identifying males and their socially mated females.

Detailed methods of recording and data manipulation are presented in Habig et al. (2019). Briefly, we video-recorded the colony for approximately 130 min d^{-1}, divided into roughly two 65-minute (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. The behaviours of the 10 focal males were later observed in the laboratory using Adobe Premiere® (Adobe Systems, San Jose, CA, USA, 2009). Videos were first observed to determine appropriate behavioural types, in order to account for all observed behaviours, with categories informed by past studies (Collias and Collias 1959; Crook 1963; Collias and Collias 1970, 1971; Roulin 1999). For each male and for each second of the 13 h of recording, the behaviour of each male was manually scored by one of us (KK), i.e. placed into one of the observed categories, excluding seconds where the male was not observed. This yielded a mean of 27 422 (±2 635) time points (seconds) for each male. These scores were then compiled using JWatcher 1.0 software (Blumstein 2010), which subsequently calculates durations and frequencies for each behaviour and assembles these data into time budgets, with standard deviation across males. Given that the total observation time varied between males, in order to compare durations between males, we standardised all durations by dividing by the mean total observation time of all 10 males. JWatcher also facilitated path analysis of behavioural sequences based on preceding and following acts, on the basis of which we created an ethogram for each male.

All behaviours (Figure 1) were observed directly except for two. When males left the breeding colony and returned with vegetation, we coded the duration of absence as *gathering nest materials*, although other behaviours, such as foraging, could also have occurred during these time periods. If they returned without vegetation, we coded the duration of absence simply as *time away*. We placed all behaviours into functional categories: behaviours related to survival versus reproduction, and amongst the latter those related to male competition versus attracting and retaining mates. We inferred that birds perched on or near their nests were defending their territories and thus engaging in male competition, based on past research on this behaviour

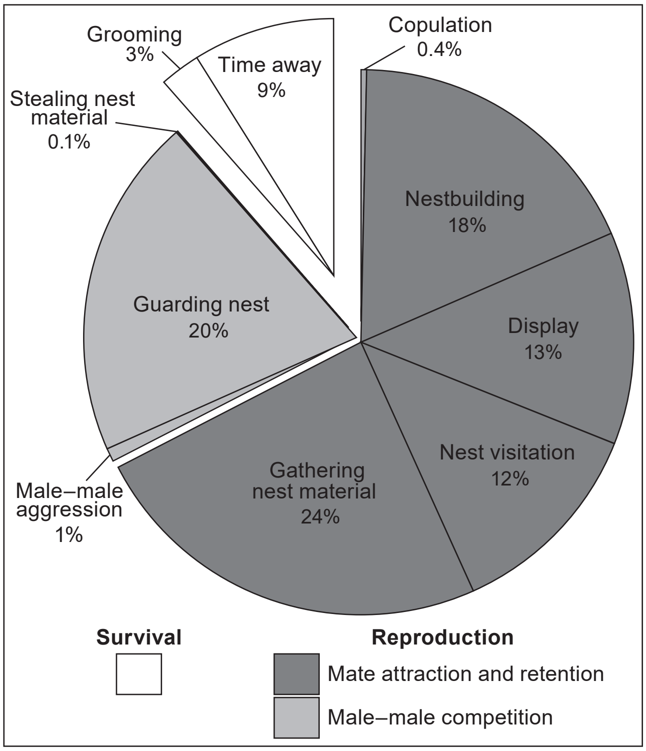

Figure 1: Overall time budget of 10 male Village Weavers *Ploceus cucullatus* in an Ethiopian breeding colony during 274 220 bird-seconds, scored each second. Recordings evenly spanned the daylight hours over a six-day period during the copulation, egg-laying and early incubation stage of breeding of the focal individuals and their mates. Values over 1% are rounded to the nearest percentage point

(Collias and Collias 1959; Crook 1963; Din 1992); this is corroborated qualitatively by the nearly constant vigilance and vocal interaction with neighbours that we observed in perching males. Nevertheless, past research also indicates that such males are also alert to intrusions from heterospecifics, such as predators and brood parasites (Habig and Lahti 2015); thus, to some extent we might have overestimated time investment in male competition.

We assessed the relationships amongst male behaviours both within males and between males. First, we performed a Pearson's correlation analysis on all pairwise comparisons of the incidence of behaviours and behavioural categories within males. In light of the strong correlations we found amongst certain behaviours, we then performed a principal component analysis (PCA) to group behaviours based on their co-occurrence. We used the results of this analysis to compare behavioural structure between males. Pearson correlations and PCA were performed using SYSTAT 10 (SPSS, Chicago, IL, USA). To compare the relative prevalence of the four functional categories (survival versus reproduction; and competition versus mate attraction), we conducted Wilcoxon matched pair tests using the 'mass' package in R (Venables and Ripley 2002).

As our recordings spanned the daylight hours evenly, we were able to test for a temporal effect on behaviour across hours. By recording these roughly synchronous breeding birds intensively over a six-day period, we aimed to minimise changes in behaviour over longer timescales reflecting differences in reproductive stage. However, we did observe that several focal males gained additional mates over the course of the study, which could have prompted changes in male behaviour. Therefore, we applied a linear mixed model (LMM) framework using Gaussian error distributions to test whether time of day, date of observation or number of resident females on a male's territory was predictive of the proportion of time a male spent on different categories of behaviour. Given that response variables were not normally distributed, we log-transformed (log + 0.5) these data. To select the best-fitting models, we applied the drop 1 function in R, and confirmed the best-fitting models using log likelihood ratio tests. All LMMs were performed using the 'lme4' (Bates et al. 2014) and 'lmerTest' (Kuznetsova et al. 2015) packages in R; male identity was modelled as a random effect. We also used a Wilcoxon matched-pair test to compare male behavioural categories during days when the minimum versus maximum number of females were resident in nests on each male's territory.

Results

We observed 10 focal Village Weaver males performing eight different behaviours at the breeding colony, in addition to time away and gathering nest materials (Figure 1). Males spent the most time gathering nest materials (24.2% ± 11.4%), perched at or near their nests guarding their territories (20.2% ± 11.5%) and nest-building (18.1 ± 8.6%). They also spent time displaying to females (12.6% ± 6.0%), visiting completed nests occupied by females (12.2 ± 4.8%), away from the colony (8.9% ± 4.5%) and grooming (2.6% ± 1.5%). Three other behaviours accounted for less than 1% of their time: engaging in aggressive interactions with each other (0.8% ± 1.4%), copulating with females (0.34% ± 0.55%) and stealing nesting materials from each other (0.06% ± 0.11%) (Figure 1).

We grouped time away and grooming as survival-related behaviours, and all the remaining behaviours as reproduction-related. Males spent much more time on behaviours related to reproduction (88.5% ± 5.6%) than survival (11.5% ± 5.4%) (Wilcoxon: $V = 3824$, $P < 0.001$; Figure 2a). Among the reproduction-related behaviours, we divided all except copulation into two subcategories: those related to male competition (guarding the nest, aggression and stealing nest materials), and those related to attracting and retaining mates (gathering nest materials, nest-building, displaying to females and visiting occupied nests). In this latter subcategory, gathering nest materials and nest-building also function as parental care. Among such reproduction-related behaviours, males spent more time on those relating to attracting and retaining mates (76.1% ± 13.5%) than to male competition (24.9% ± 11.1%) (Wilcoxon: $V = 3588$, $P < 0.001$; Figure 2b).

The amount of time males spent performing any given behaviour did not change consistently hour-to-hour over the course of the day (LMM: $P > 0.2$ in all cases). Over the six days of observation, LMM indicated that males tended to decrease time spent on certain behaviours: copulation (estimate: −0.155, $p = 0.047$), gathering nest materials (estimate: −0.753, $p < 0.001$), nest-building (estimate: −0.538, $p < 0.001$), displaying to females (estimate: −0.550, $p < 0.001$) and aggression behaviours (estimate: −0.388, $p < 0.001$). Over the same period, males tended to increase time spent on visiting nests (estimate: 0.077, $p = 0.002$) and grooming (estimate: 0.516, $p < 0.001$). Overall, the time a male spent displaying to females was positively related to the number of mates resident on his territory (estimate: 1.074, $p = 0.018$).

Seven of the 10 males increased their number of mates over the course of the study, in terms of females residing

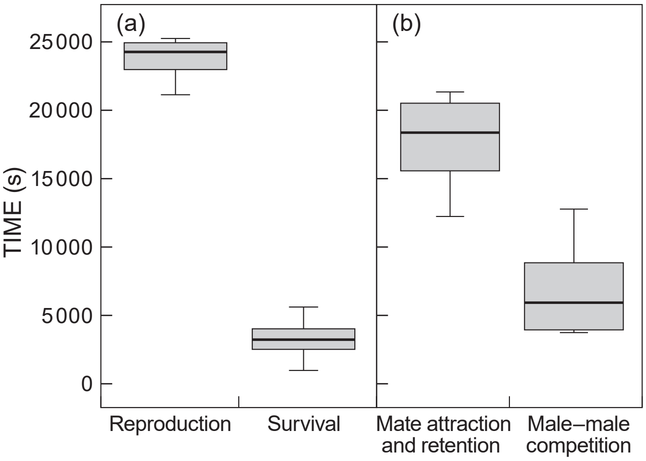

Figure 2: Boxplots of Village Weaver behaviour at a breeding colony by functional category. Males spent more time engaging in reproduction-related than survival-related behaviours (a), and spent more time on behaviours related to mate attraction and retention than those involving male–male competition (b)

in nests the males had built. Comparing days on which these males had the minimum (1–2) versus maximum (3–4) number of resident females, as males acquired additional mates they tended to increase survival-related behaviours (Wilcoxon: $V = 2$, $P = 0.047$; Figure 3a) and male competition (Wilcoxon: $V = 1$, $P = 0.031$; Figure 3b), but tended to decrease reproduction-related behaviours (Wilcoxon: $V = 26$, $P = 0.047$; Figure 3c), particularly those related to female choice (Wilcoxon: $V = 27$, $P = 0.031$; Figure 3d). The specific behavioural changes contributing most heavily to this effect were a decrease in gathering nest materials and nest-building (Figure 3e). However, all seven males spent more time visiting nests when they had more mates (Figure 3f).

Pairwise comparison of time spent performing specific behaviours revealed a few moderate to strong correlations (Table 1). These can be reduced to two patterns. First, the three behaviours related to male–male competition (nest guarding, aggression and stealing nest materials) were all strongly positively correlated with each other ($r > 0.75$), and each of these three competitive behaviours was negatively correlated with gathering nesting materials and nest-building ($r < -0.61$). Second, the reproductively early behaviours of gathering nest materials and nest-building were positively correlated ($r = 0.62$); the later functional behaviours of displaying beneath the nest and visiting nests after females take up residence in them were positively correlated ($r = 0.58$), whereas both of these were negatively correlated with nest-building ($r < -0.58$).

An unrotated PCA reduced the data to two components that were concordant with the correlation results. PC1, which explained 45.7% of the variation, reflected a high incidence of male–male competitive behaviour (nest-guarding, aggression and stealing nest material) and a low incidence of gathering nest materials and nest-building. PC2, which explained a further 19.2% of the variation, reflected a high incidence of time away and grooming, and a low incidence of courtship behaviours (displaying and nest visitation) (Figure 4). Focal males varied continuously on both axes (Figure 5).

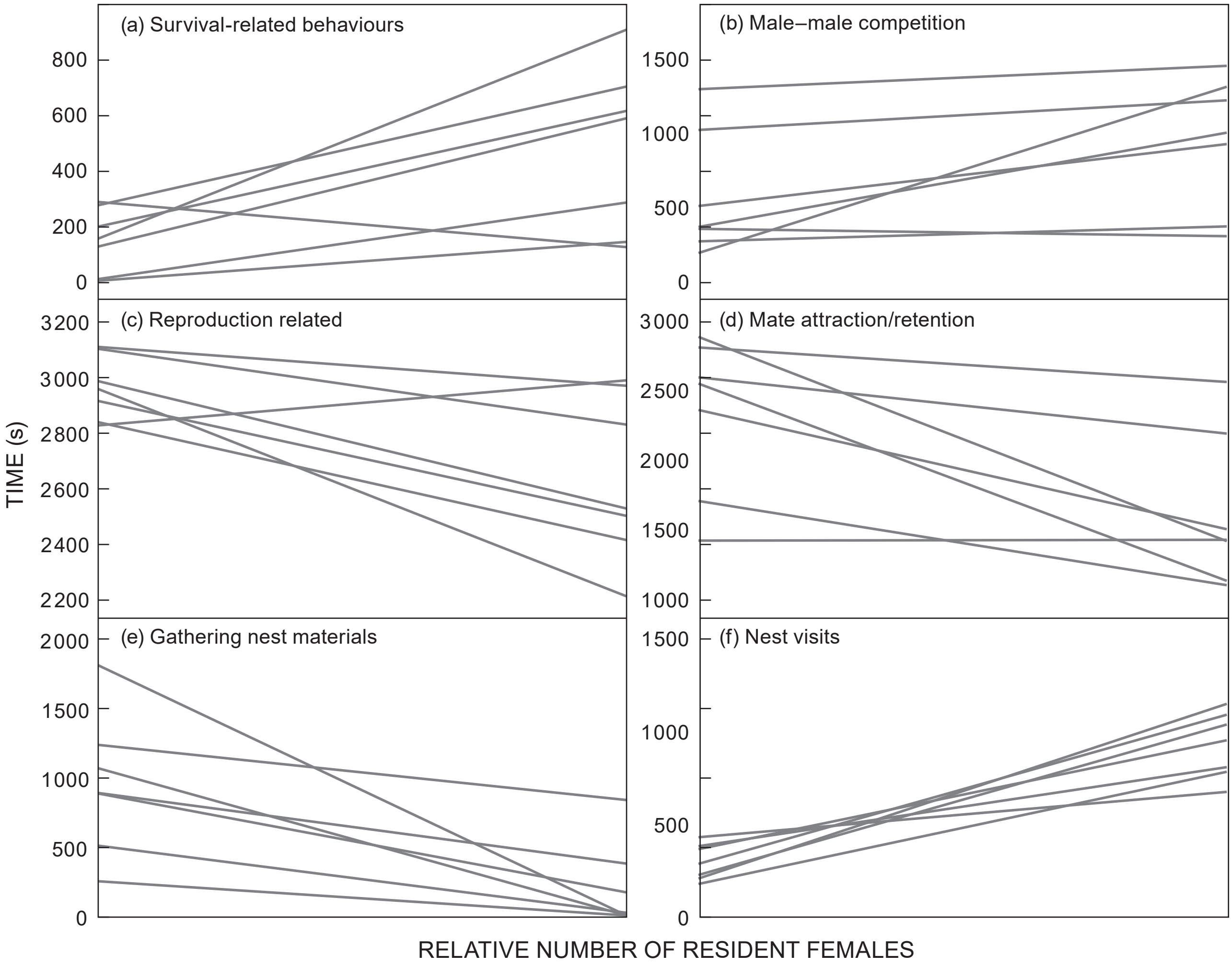

Figure 3: Change in Village Weaver behaviour within individual males from when the minimum (left edge of graphs) to the maximum (right edge of graphs) number of females took up residence on each male's territory, over the duration of the study. Males increased behaviours related to individual survival (a) and male–male competition (b), but tended to decrease reproduction-related behaviours in general (c), especially those involved in acquiring and retaining mates (d). Males decreased the time spent gathering nest materials (e) and increased the time spent visiting nests (f)

Table 1: Pairwise correlation coefficients between behaviours performed by 10 male Village Weavers in a breeding colony, in terms of the time individuals spent performing each behaviour during 13.5 h over a six-day period. Moderate to strong correlations (< –0.5 and > 0.5) are in bold

Behaviour	Nest-building	Copulating	Displaying	Nest visitation	Time away	Gathering nest materials	Grooming	Aggression	Stealing nest materials
Copulating	−0.333								
Displaying	**-0.684**	0.372							
Nest visitation	**-0.584**	0.214	**0.580**						
Time away	–0.274	–0.058	0.100	–0.104					
Gathering nest materials	**0.615**	–0.433	**-0.532**	–0.401	–0.252				
Grooming	0.181	–0.065	–0.038	–0.101	0.440	–0.444			
Aggression	**-0.691**	0.215	0.200	0.247	0.057	**-0.674**	0.158		
Stealing nest materials	**-0.880**	0.015	0.261	–0.015	0.383	**-0.614**	0.325	**0.864**	
Nest guarding	**-0.666**	0.484	0.247	0.179	0.128	**-0.784**	0.195	**0.911**	**0.752**

Path analysis revealed only moderate tendencies across individuals in the behavioural sequences of males (Figure 6). Individuals building nests often alternated bouts of construction with trips out of the colony (0.49) or grooming (0.42); and after nest-guarding, a male would often (0.38) leave the colony. Notably, nest-building did not follow stealing of nest materials. The relationship between proportional duration and frequency of behaviours can be assessed by comparing Figures 1 and 6. For instance, males gathered nest materials 0.24 of the time by duration but 0.016 by frequency, indicating a much longer bout length than time away more generally, which was 0.09 by duration and 0.238 by frequency. Thus, males that left the colony for a longer time tended to be gathering nest materials, and spent on the whole 2.7 times longer (0.24/0.09) doing so; however, males left the colony 15 times as often (0.238/0.016) without gathering nest materials.

Discussion

Results of this observational study on the time budgets of Village Weavers at the height of breeding are consistent with the prediction that sexual selection is intense in polygynous and colonial birds. Males spent about 88% of their time on behaviours that function in obtaining or retaining mates. Of such sexually selected behaviours,

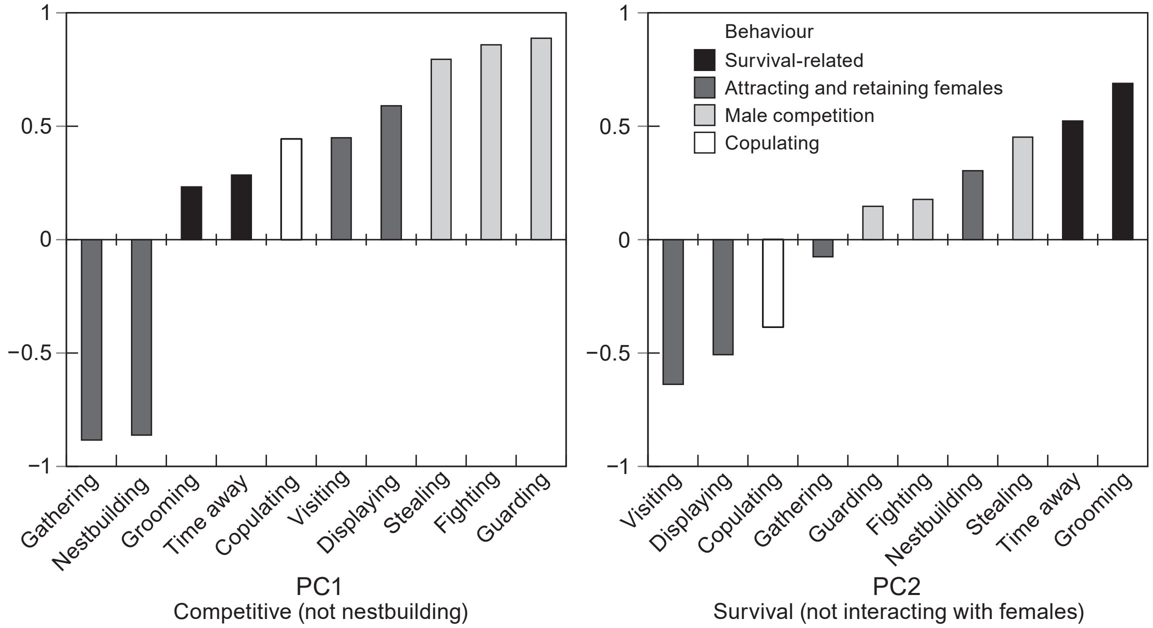

Figure 4: Loadings of the first two principal components on 10 behaviours of male Village Weavers, explaining 45.7% and 19.2% of the variation, respectively. A high PC1 score indicates a high incidence of competitive behaviours and a low incidence of nesting behaviours; a high PC2 score indicates a high incidence of survival-related behaviours and a low incidence of attention to females. Black bars are survival-related behaviours; dark grey bars are behaviours involved in attracting and retaining females; light grey bars are behaviours relating to male competition

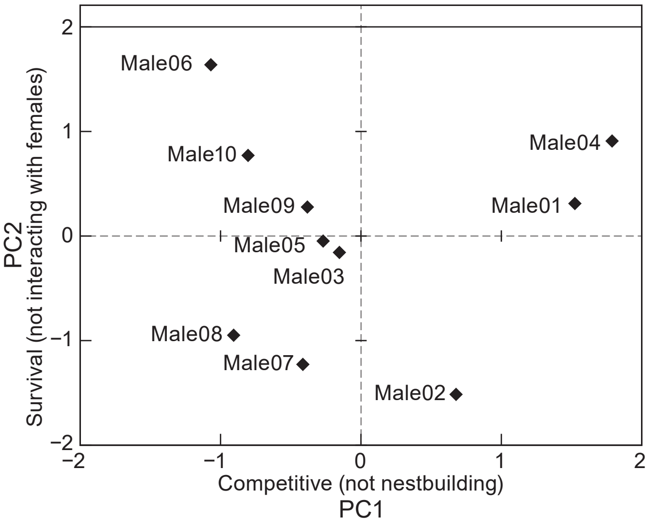

Figure 5: Behavioural phenotypes of each focal male Village Weaver with respect to the two principal components described in Figure 4. Males exhibited continuous variation in both broad behavioural features: the tendency to compete with other males versus building nests (PC1), and the tendency to pursue survival-related behaviours versus attending to females (PC2)

those relating to female choice (nest-building, displaying and attending to females) accounted for 76% of the temporal investment, with the other 24% being devoted to male competition (aggression and nest material stealing/sabotage).

Males with more mates displayed more at their nests, although we cannot determine whether a higher display rate attracts a higher number of mates, or if displays function in mate retention. A given male varied his behaviour as a function of his mating status. Males who increased their number of mates over the period of observation increased the time they devoted to nest visitation, but their investment in gathering nest materials fell precipitously. Overall, these males shifted to devoting more time to male competition and survival and less to female choice, despite the increase in nest visits. These changes in behaviour following an increase in mates add to previous findings focusing on male behaviour following a colony disturbance: Habig et al. (2017) found that in these situations males fled the colony less often and returned to the colony sooner after increasing their number of mates.

Correlations demonstrated the functional relationship amongst behaviours involved in male competition (guarding, aggression and stealing), as well as a tradeoff

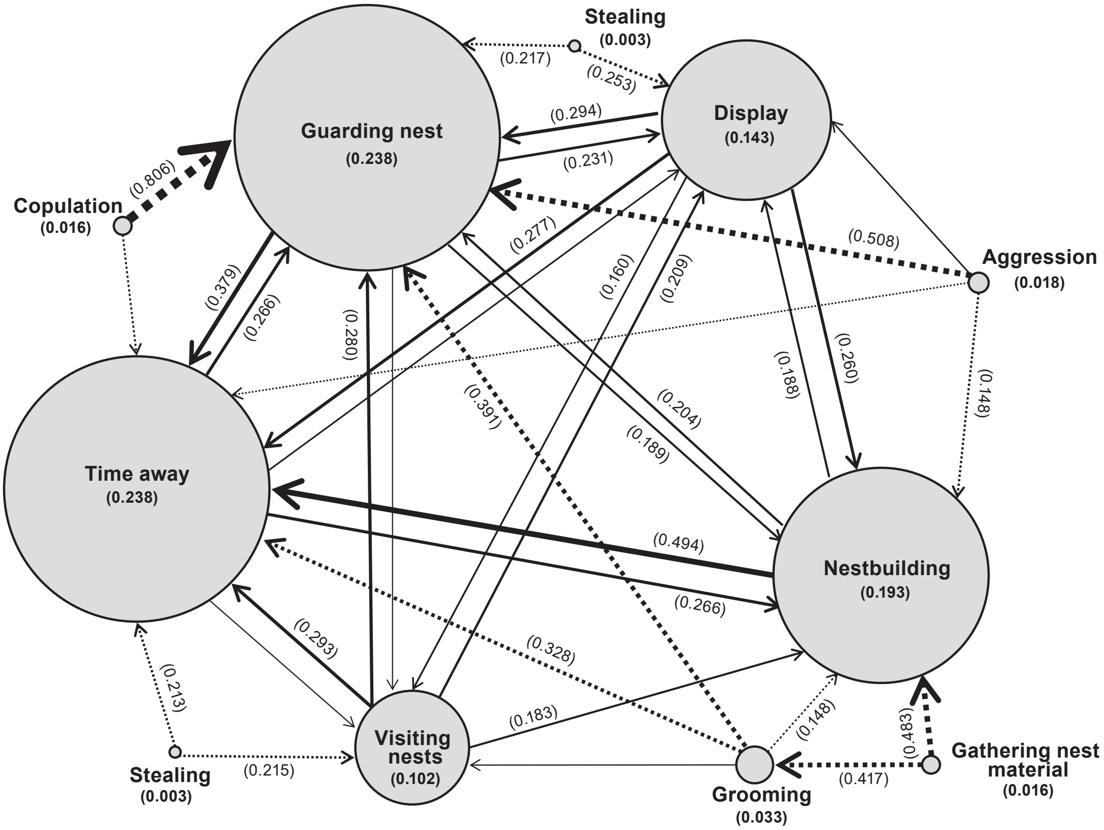

Figure 6: Ethogram illustrating the frequency of performance of behaviours and the proportional incidence of preceding and following acts, averaged across 10 Village Weavers during 13.5 h of video-recording over six days. The diameter of each circle (and the associated number) indicates the frequency of performance of that behaviour, without regard to duration; i.e. a value of 0.1 for behaviour X means that when an individual changed behaviour, 10% of the time the new behaviour would be X. The thickness of each arrow indicates the transition probability between different behaviours. Transition probabilities over 0.15 are labelled; transition probabilities between 0.10 and 0.15 are represented with unlabelled arrows; transition probabilities less than 0.10 are not shown. Transitions from behaviours with frequencies <0.05 are represented by dotted lines because probabilities are less reliable. The behaviour of 'stealing' (nest materials) is represented twice to reduce clutter—the total frequency of stealing was 0.003

between these and investing in one's nest; this was borne out by the PCA as well, with this set of relationships explaining over 45% of the observed behavioural variation. Thus, males did not generally attempt to build their nests while guarding. Moreover, some males stole nesting materials and some did not, but those that did engage in this behaviour were not appropriating materials for their own nests: as the path analysis shows, males did not engage in nest-building after stealing. More generally, males that stole nesting material spent less time gathering nest materials and building than males that did not steal. This negative relationship was not due to a time constraint, as stealing nesting materials occupied only a small portion of any male's time. In addition, the more time a male spent behaving aggressively toward other males, the less time he spent investing in its own nest, despite again the small absolute amount of time any male devoted to aggression.

Behaviours related to constructing nests were inversely correlated with nest displays and visits, which themselves were positively correlated. This set of relationships appears to reflect a temporal sequence of functionality, with nest-building being important in a prior stage of a given male's breeding attempt and attention to females being functional subsequently. Moreover, the female-directed behaviours of displaying and nest visitation trade off with the survival-related behaviours of foraging (likely the main undetected function of leaving the colony) and grooming; this explained 19% of all observed behavioural variation according to the PCA.

The behavioural relationships we found do not translate into rigid sequences of performance according to the path analysis; nor do individual males fall out into simple categorical areas of a map of behavioural variation despite the strong relationships amongst behaviours. Moreover, temporally varying features such as date of observation, number of mates, and the order in which behaviours are functional all influenced male behaviour; therefore at least some of the variation we observed between males might simply be due to circumstances and could change over time. The two-dimensional map of behavioural variation that an unrotated PCA identified as maximally explanatory (Figure 5) can be distilled into four functions: (a) survival, (b) competition with rivals, (c) nest construction and (d) attending to females, such that each quadrant represents the positive contribution of two of them. Individual Village Weavers appear to vary continuously in this space. Whether individual differences qualify as variation in personality (e.g. Dall et al. 2004) is unknown; testing this would require following individual males over longer periods of time.

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