



Original Article

Male risk-taking is related to number of mates in a polygynous bird

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Evolutionary theory predicts that when intrasexual competition is intense, risky behaviors can evolve if they enhance reproductive success. Here we tested the idea that polygynous males exhibit predictable variation in risk-taking during intense competition for mates. We conducted an observational study of a village weaverbird (*Ploceus cucullatus*) breeding colony, and video recorded synchronous fleeing events, a common predator avoidance behavior. Males adjusted their flight from the colony according to the amplitude (loudness) and Wiener entropy (harshness) of conspecific alarm calls during a perceived threat. Males also varied in how often they fled the colony. Specifically, in line with predictions based on the value of a male's territory, males with more nesting females were less likely to flee, and returned sooner if they did flee, compared to males with fewer nesting females. Males with a nest under construction also returned to their nests sooner than males without constructions in progress, consistent with predictions based on nest sabotage by conspecifics. These results suggest that male weavers perform a cost-benefit analysis in real time in order to decide how to respond to a perceived threat, with self-protection trading off with the security of one's territory and mates.

INTRODUCTION

The propensity of certain individuals to engage in risky behavior is an evolutionarily intriguing phenomenon. Life history theory predicts that such behavior, if widespread, should maximize the outcome of a fitness tradeoff (Ghalambor and Martin 2002, Bell 2007, Wolf et al. 2007). The benefits secured by engaging in risky behavior should counteract the costs of not being cautious (Houston and McNamara 1999). For instance, extravagant ornaments, boldness, and fighting ability, while presumably leading to an increased risk of predation (Darwin 1871, Zuk and Kolluru 1998, Cooper 1999), may nevertheless improve reproductive success in the context of competition for mates (Darwin 1871). Moreover, variance in reproductive success in males of many species is higher than in females. Thus, males tend more often to be risk-takers (Trivers 1972) and often adopt a “live hard, die young” strategy (Zuk 1990). In terms of fitness, risk-taking can be thought of as a high-cost, high-return strategy whereas risk-aversion can be thought of as a low-cost, low-return strategy (Lima and Dill 1990). Studies on several taxa have demonstrated that males tend to take more risks than females (e.g., Breitwisch and Hudak 1989; Videler et al. 2015; but see Fernandez et al. 2015), and that risky behavior tends to be more prevalent in

the breeding versus the non-breeding season (e.g., Boukhriss and Selmi 2010; Eccard and Herde 2013; Magnhagen et al. 2014).

Variation in risk-taking behavior has been documented recently in many taxa, including invertebrates (Brown et al. 2012; Mowles et al. 2012; Muller 2012; Cordes et al. 2013, Videler et al. 2015), fish (e.g., Ruiz-Gomez and Huntingford 2012; Castanheira et al. 2013; Laine et al. 2014; Magnhagen et al. 2014), squamates (Cooper 2009, 2012; Kuo et al. 2015), birds (e.g., Yoon et al. 2012; Brust et al. 2013; Miller et al. 2013; Møller et al. 2013; Fernandez et al. 2015), and mammals (Dammhahn and Almeling 2012; Bonnot et al. 2013; Eccard and Herde 2013; Longman-Mills and Carpenter 2013; Halliday et al. 2014). Studies have assessed variation between species (e.g., Møller and Garamszegi 2012; Møller and Liang 2013; Møller et al. 2013), at the population level (e.g., Thomson et al. 2011; Dassow et al. 2012; Magnhagen et al. 2012; Bonnot et al. 2013), and at the individual level (Byrnes et al. 1999; Cooper and Wilson 2007; Pawlowski et al. 2008; Eccard and Herde 2013). At the individual level, considerable research has centered on the boldness-shyness continuum (Wilson et al. 1994), and on the relationship between personality or temperament (i.e., behavioral syndromes) and behavioral plasticity (e.g., Sih et al. 2004; Neff and Sherman 2004; Réale et al. 2007; Dingemanse et al. 2010; Magnhagen 2012; Mowles et al. 2012; Nicolaus et al. 2012; Wolf and Weissing 2012; Brust et al. 2013; Castanheira et al. 2013). Most of the above studies have been conducted in the

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laboratory or under semi-natural conditions, although a few studies have been conducted in the wild under natural conditions (e.g., Cimprich et al. 2005; Natoli et al. 2005; Chiyo et al. 2011; Bonnot et al. 2013). Typically, laboratory studies can assess costs and benefits rather well, but establishing biological relevance is challenging; whereas on the other hand nonintrusive observational studies in the wild have plausible biological relevance, but at the expense of effective detection of causality. In the present study, we assessed natural individual variation in the risk-taking behaviors of the village weaverbird (*Ploceus cucullatus*), a colonial, polygynous bird (Crook 1963, Collias and Collias 1967, 1970), and test for the relation of such behavior to available current proxies for individual cost and benefit.

In many bird taxa, including weavers, synchronous flights—i.e., “dreads” or “panic flights”—are commonly employed anti-predatory behaviors (e.g., Marples and Marples 1934; Palmer 1941; Emlen et al. 1966; Veen 1977; Meehan and Nisbet 2002; Habig and Lahti 2015). We used these synchronous flights, which were first described in weavers by Chapin (1954), to quantify risk-taking behavior in male village weavers under thoroughly natural conditions. While many of these flights result in “false alarms” (Habig and Lahti 2015), the decision to remain on a territory when alarm signals are elicited by conspecifics is risky as evidenced by previous studies documenting predation of adult weaverbirds by avian heterospecifics on their respective colonies (Collias and Collias 1959, 1970; Ginn 1991). Only one other known study has used naturally observed synchronous flights to assess risk-taking behavior: a house sparrow (*Passer domesticus*) study that compared risk-taking between males and females (Breitwisch and Hudak 1989). In that study, the authors employed artificial experimental conditions (baiting). In the present study, we use video observation of a village weaver colony from a distance to assess natural variation in male risk-taking between and within individuals during breeding. Specifically, we measured the responses of males to natural colony-wide disturbances or intrusions that instigated *synchronous fleeing events*, striking phenomena when over 75% of the visible members of the colony suddenly flee (Habig and Lahti 2015).

We expected males to allocate effort and weigh risks according to the relative fitness value of behavioral alternatives (Smith 1995). For instance, a male should be more motivated to risk predation, to stay and defend his territory (whether from predators or competitors) when that territory is more valuable (Montgomerie and Weatherhead 1988). Village weaver males defend territories within their breeding colony, and build nests and attempt to attract females to take up residence in them. Therefore, we predicted that a male will engage in risky behavior during and following colony-wide disturbances according to territorial “resources”, i.e., the number of his nests and the number of females occupying them. We measured risk-taking in this context as how often a male remains on his territory during a synchronous fleeing event and, if the male does flee, how soon he returns relative to other individuals. We predicted that males with more nests or more females would be less likely to flee the territory and would return sooner than males with fewer nests or females. However, an alternative basis for this prediction, at least with regard to the number of females, is that females might already have chosen bolder males with which to mate (Reaney and Blackwell 2007). Thus we also measured whether individual males changed their level of risk-taking according to the number of female residents in their respective territories on different days. If males adjust their behavior to current costs and benefits, the same male will be more risky when he has more females than when he has fewer females; if on the other hand, the association is due to female choice of bolder or

older males, then male behavior is not expected to change based on the number of resident females.

Risk-taking behavior should be sensitive not only to perceived benefits but also costs (Hedrick and Kortet 2012). A previous study (Habig and Lahti 2015) found that the “many eyes” of a weaverbird colony was associated with synchronous fleeing events, and that many of these events are “false alarms” in that the intruding species was innocuous. The contagious nature of these flights is such that individuals tend to flee the colony simultaneously, rather than looking around to independently assess the nature of the disturbance or intrusion. The main opportunity a weaver has to assess the cost of staying versus fleeing appears to be the alarm call usually given by one or more individuals immediately before the synchronous fleeing event. Previous studies of alarm calls in captive and wild village weavers found such vocalizations to be associated with specific negative stimuli including the approach of a human, hawks diving towards a colony, handling of an individual, and the attack of one weaver by another (Collias 1963, 2000). Four acoustic features have been associated with high intensity alarm in weaverbirds: longer duration, higher frequency, harsher tonality, and higher amplitude (Collias 1963, 2000, Collias and Collias 2004). Thus, we hypothesized that weavers adjust their risk-taking behavior to the perception of cost during a colony-wide disturbance via assessment of these alarm-related acoustic features. Once having fled, these features will cease to be informative, so males should use other information (including the value of their territories) to assess the cost of returning.

METHODS

We studied a breeding colony of village weaverbirds (*P. c. abyssinicus* Gmelin 1789) in July–August 2010 in Awash National Park in Ethiopia (9.33°N, 40.33°E). The colony, which was located in a fig tree (*Ficus* sp.) on the edge of the Awash River adjacent to a sugar plantation, consisted of over 100 nests and filled the main volume of the tree. We randomly selected 10 males as focal subjects of our observational study. We identified the territories of the 10 focal males in this colony on the basis of all nests being clearly distinguished and the males performing inverted wing-flapping displays while hanging from them; male village weavers display only from their own nests (Crook 1963; Collias and Collias 1970, 1984). We were also able to identify the females residing within each focal male’s territory based on behavioral cues: following the investigation and subsequent acceptance of a nest, a female copulates with the resident male, lines the nest with vegetation, and reliably returns to the same nest for the remainder of the breeding cycle (Collias and Collias 1959, 1970, 1984). A male will subsequently attack other females who attempt to gain access to the nest (unpublished data). Thus both males and females could be reliably identified on breeding territories without marking.

We recorded the 10 focal males using a Canon VIXIA HF S21 camcorder at high definition (1920 × 1080 px). Recordings were taken during daylight hours, when peak predation is likely (e.g., Libsch et al. 2008) and when the weavers are most active (Collias and Collias 1970). Recordings were divided into 2 approximately 65-min periods at different times of day (mean = 66.94; SD = 9.7). By the end of the sixth day, we completed 13 h of recording encompassing all daylight hours (between 0630 and 1930). During the recordings, the camera was positioned in the same location daily, 20 m from the colony across the Awash River, among littoral vegetation. The high definition videos were studied using

Adobe Premiere (Adobe Systems Incorporated, 2009): the individual behaviors of the 10 territorial males and 30 associated females were observed in slow motion and coded every second. When we observed focal females lining their respective nests with vegetation (and no longer copulating with a territorial male), we were also able to determine that they were in either the egg-laying or early incubation stages of breeding during the video recordings (Collias and Collias 1959, 1970, 1984).

During the video observations, we noted all occurrences of a synchronous fleeing event (Habig and Lahti 2015), which was defined as any episode in which a minimum of 75% of the weavers visible in the video camera's field of view (henceforth "visible") fled the colony instantaneously (within 2 s). For each event, we played back the video in slow motion and recorded the number of visible males and females at 60 s, 30 s, and 10 s before the fleeing event. We then recorded the number of males and females that did not fly away but remained in the colony at the time of the event (time zero). Lastly, we recorded the number of visible males and females that were present in the colony 10 s, 30 s, and 60 s following the event.

We quantified 2 metrics associated with male risk-taking: *fleeing probability* and *order of return* during and after a synchronous fleeing event. With regard to fleeing probability, we assigned each individual male a score of 1 if he fled during a colony-wide disturbance and a score of 0 if he remained in the territory. We considered males with a lower fleeing probability to be greater risk-takers. We measured order of return by counting the sequence in which focal males returned to the colony following a synchronous fleeing event. The first male that returned following a disturbance was assigned a 1, the second returning male was assigned a 2, and so on. We considered males who returned to their territories sooner to be greater risk-takers. We assessed the relationship between these measures of risk-taking and 2 factors: number of nesting females and whether or not a nest was under construction.

Audio was recorded over the entire length of the video recording (Canon DM-100 directional stereo microphone). Sound files (in uncompressed wav format; sampling rate 44.1 kHz; 16-bit; 1-min bin) were analyzed using 2 programs: 1) Raven Pro 1.4 (Cornell Laboratory of Ornithology, Ithaca, NY) for amplitude, frequency, and duration of vocalization and 2) Sound Analysis Pro (Tchernichovski 2000) for Wiener entropy. While multiple birds produced calls prior to a fleeing event, as shown in Supplementary Table S1, we identified the final, nonoverlapping vocalization immediately preceding a synchronous flight. For each of these vocalizations we determined minimum and maximum frequency (kHz), duration (s), maximum amplitude (kilounits), and Wiener entropy (log scale). Measures of signal amplitude in nature are subject to various sources of environmental and individual variation that are not related to function (e.g., wind, obstacles, and the orientation of the caller in relation to the microphone). Some random variation was mitigated by the general loudness of the vocalizations we measured, and the fact that the microphone was virtually equidistant from all members of the colony.

We used a generalized linear mixed model framework (Bolker et al. 2009) to determine factors influencing fleeing probability. Fleeing (dependent variable) was represented as a binary variable where a value of one indicated a male that fled, and zero indicated a male that did not flee, during each event. We included as independent variables 2 attributes of each male's territory known to be associated with fitness (Montgomerie and Weatherhead 1988, Lind and Cresswell 2005): 1) number of nesting females and 2) whether or not a nest was under construction. We also included

as independent covariates several features of calls immediately preceding a colony-wide disturbance: 1) duration, 2) frequency, 3) Wiener entropy, and 4) amplitude. These features are potentially indicative of the fitness cost of a colony intrusion (Collias 1963, 2000; Collias and Collias 2004).

We considered several models, with different combinations of independent variables, including an intercept-only model, a saturated model with all 6 variables, and unique combinations of 2 to 5 variables. The best of the 64 candidate models was considered to be the one with the smallest Akaike Information Criterion (AIC) value (Burnham and Anderson 2004). Male identity was incorporated as a random effect to minimize inflation of *P* values due to pseudoreplication. Because individual males may also vary in risk-taking due to age differences or other unmeasured personality attributes, we evaluated the significance of a model involving male identity as a random effect with a model without random effects using Analysis of Variance (Anova). Since model comparison using Anova can be conservative because of the boundary problem of random effects, we also evaluated change in coefficients and probability values in our models as a result of inclusion of these random effects. Additionally, we tested whether day of observation as a random effect was significantly different from the simple model without day of observation as a random effect using Anova. We evaluated the influence of random effects using the best covariate model. The GLMM analyses above were conducted using the *glmmadmb* package (Fournier et al. 2012) in the R project for Statistical Computing (R Core Team 2012).

To determine factors influencing the order of return following a colony-wide disturbance, we used a cumulative linked mixed model (CLMM) framework. We included order of return as a dependent variable and considered separate models with all possible combinations of the 6 independent variables. Male identity and the day of observation were included in the model as random effects jointly or separately to account for repeated measures on the same individuals and any effects due to variation in group size during each observation. We compared the models including random effects with simple models without random effects using Anova, and examined their effects on regression coefficients. AIC was used to select the most parsimonious model (Burnham and Anderson 2004). We performed the clmm using the *ordinal* package (Christensen 2011) in the R project for Statistical Computing (R Core Team 2012).

Lastly, to disentangle any age or individual male effects from the influence of other covariates, we performed post-hoc analyses using Wilcoxon matched pairs tests. Specifically, we compared the probability of fleeing when a male's territory was occupied by the minimum versus the maximum number of females during the period of observation, in order to test whether individual male behavior varied with mating success.

RESULTS

The 10 territorial males possessed a mean of 2.08 nests (SD = 0.84; range: 0–4) and defended a mean of 1.93 females (SD = 0.83; range: 0–4) throughout the study duration. The mean number of nests under construction per male throughout the observation period was 0.45 (SD = 0.41; range: 0–1). On the last day of observation, the mean number of nests per male was 2.80 (SD = 1.40; range: 0–4) and the number of associated females per male was 2.60 (SD = 1.35; range: 0–4). The proportion of built nests that were occupied by females on the last day of observation was 0.93.

Thirty-six synchronous fleeing events occurred during the period of observation. The average median duration of absence per

fleeing event (the amount of time between the synchronous flight and the point at which half the number of birds that had fled returned to the colony) was 67.6 s (SD = 126.6; range: 2.03–561.6). The mean duration of absence for males who fled during colony-wide disturbances was 139.7 s (SD = 31.4). Fleeing duration ranged from a minimum of 2.0 s to a maximum of 1277 s.

The mean amplitude (loudness) of alarm vocalizations was 4339 kilounits (SD = 1340; range: 1936–7204), the mean minimum frequency was 3.4 kHz (SD = 0.97; range: 2.1–6.8), the mean maximum frequency was 5.4 kHz (SD = 1.1; range: 3.4–8.3), the mean duration of vocalization was 0.2 s (SD = 0.31; range: 0.01–1.89), and the mean entropy was -1.9 (SD = 0.33; range: -2.6 to -1.2). Data broken down by fleeing event are listed in Supplementary Table S1.

The number of visible males in the colony compared to females was consistently greater in all situations. On average, 19.25 males (SD = 7.01; range: 5–36) and 1.31 females (SD = 1.47; range: 0–6) were visible 10 s before a fleeing event, 0.06 females (SD = 0.23; range: 0–1) and 2.28 males (SD = 2.37; range: 0–6) were visible during time zero of a fleeing event, and 9.22 males (SD = 7.37; range: 0–24) and 0.14 females (SD = 0.35; range: 0–1) were visible 10 s following a fleeing event.

Throughout the observation period, a mean proportion of 0.88 (SD = 0.09) males fled during a perceived threat to the colony; thus, males took risks by not fleeing on average 11.7% of the time when there was a synchronous fleeing event. The “boldest” male weaver fled during 72.0% of the disturbances and the most “fearful” 3 males fled in 100% of the events. A GLMM showed that fleeing probability of a male was best predicted by a model with 3 variables: 1) the number of female residents on his territory, 2) the maximum amplitude, and 3) Wiener entropy of the vocalization immediately preceding the event (Figure 1a–b; Table 1; Supplementary Figure S1a–b; Supplementary Figure S2). Specifically, a male was significantly less likely to flee during a colony-wide disturbance when there were more nesting females

residing on his territory, and was more likely to flee the higher the maximum amplitude and the harsher the tonality (the higher the Wiener entropy) of the call immediately preceding the fleeing event. Other supported models ($\Delta_{AIC} < 2.0$, Supplementary Table S2) likewise included variables 1 and 2 above. The simplest supported model included the number of females on a male’s territory and maximum amplitude as predictor/independent covariates. Three of the supported models had one additional variable in addition to the 3 in the best model and these were maximum frequency, duration of vocalization, and number of nests under construction (Supplementary Table S2). Comparing our best model with male ID or observation as random effects, we observed a marginally significant effect of male ID (Deviance = 3.523, $df = 1$, $P = 0.060$) but no effect for day of observation (Deviance = 0, $df = 2$, $P = 1$) or a combination of male ID and observation (Deviance = 3.523, $df = 2$, $P = 0.171$). Similarly the variance in fleeing probability was larger using male ID as a random effect (SD = 0.763) compared to when observation day was used as a random effect (SD = 0.001). Fleeing probability within an individual male was significantly higher on days when the minimum number of females were residents on his territory (mean: 0.91; SD = 0.10), compared to the maximum number of females (mean: 0.71; SD = 0.30; Wilcoxon’s statistic $V = 27$, $P = 0.03461$).

The mean order of return of males following a synchronous fleeing event was 3.65 (SD = 0.88). The “boldest” male had an ordinal return average of 2.72 while the most “fearful” male had an ordinal return average of 5.62. CLMM analyses showed that the number of females residing on a male’s territory and whether a nest was under construction were the best predictors of a male’s order of return following a synchronous fleeing event (Figure 2; Table 2). Specifically, males were significantly more likely to return sooner if there were more females residing on his territory or if he was in the process of constructing a nest. Other models with additional sets of predictors to those included in the best model were also supported ($\Delta_{AIC} < 2.0$, Supplementary Table S3). These additional predictors

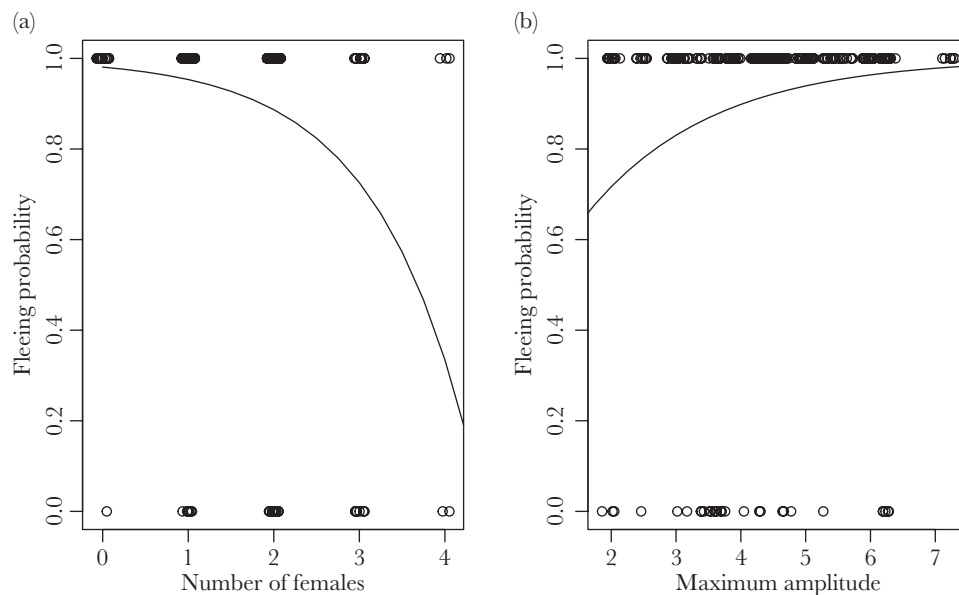


Figure 1

Regression curve indicating that the probability of a male fleeing during a colony-wide disturbance (a) decreases with the number of females residing on his territory (GLMM: $n = 247$; $\beta = -0.886$; SE = 0.302; $P = 0.0033$) and (b) increases with the maximum amplitude (loudness) of the vocalization in the colony immediately preceding the synchronous fleeing event (GLMM: $n = 247$; $\beta = 0.514$; SE = 0.193; $P = 0.0078$).

Table 1
Generalized linear mixed model of the best predictors of male fleeing

Variable	Estimate	SE	<i>z</i>	<i>P</i>
Intercept	4.242	1.454	2.92	0.0035
Number of females	-0.886	0.302	-2.93	0.0033
Maximum amplitude	0.513	0.193	2.66	0.0078
Entropy	1.325	0.727	1.82	0.0683

Coefficients for covariates best predicting fleeing probability (GLMM). Male ID was modeled as a random effect (SD=0.7629). For comparisons with other models, please see Supplementary Table S2.

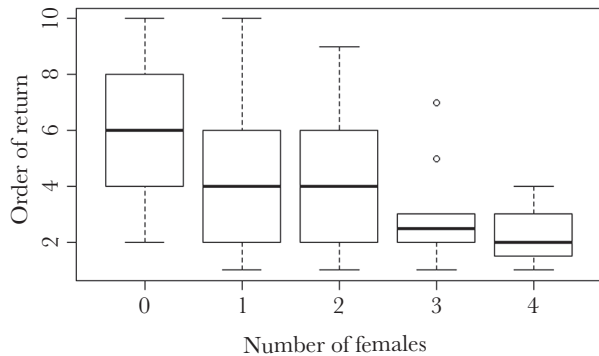


Figure 2
Box plot of order of male return following a colony-wide disturbance as a function of number of females currently residing on each male's territory. Males return sooner when they have more females (CLMM: *n* = 218; $\beta = -0.420$; SE = 0.106; *P* < 0.0001). In this figure, the median is indicated by the horizontal line, the range is represented by the vertical distance between the smallest and largest values, and the interquartile range is represented by the length of the box.

Table 2
Cumulative Linked Mixed Model (CLMM) of the best predictors of male order of return following a colony-wide disturbance

Variable	Estimate	SE	<i>z</i>	<i>P</i>
Number of females	-0.4199	0.1057	-3.972	<0.0001
Nests under construction	-0.4051	0.1595	-2.54	0.0111

Coefficients for covariates best predicting order of return following a colony-wide disturbance (CLMM.) Male ID was modeled as a random effect (SD=0.000045). For comparisons with other models, please see Supplementary Table S2.

included maximum amplitude, entropy, duration of vocalization, and maximum frequency. Using our best model to evaluate random effects by comparing a simple model without random effects, a more complex model was not supported. Within an individual male, mean order of return was lower on days when the minimum number of females were residents on his territory (mean = 3.05; SD = 1.30), compared to the maximum number of females (mean: 4.11; SD = 0.80), although this difference was not statistically significant (Wilcoxon's *V* = 25, *P* = 0.3598).

DISCUSSION

Colonially breeding village weaverbirds vary in their risk-taking behavior, and this variation is consistent with expectations based on cost-benefit trade-offs. When a colony was disturbed, males fled

88% of the time (range 72–100%). A male was more likely to flee the harsher or louder the call that immediately preceded a disturbance, and was less likely to flee if there were more mates residing on his territory. Once having fled, a male would return to the colony sooner if he had more mates or a nest under construction. The variation in male risk-taking during a disturbance as a function of mating success was dramatic: according to the best-fit model predictions, a male with zero females would flee any time there is a synchronous fleeing event, whereas a male with 4 females in his territory would remain in his respective territory 44% of the time.

The primary indication of the magnitude of a risk represented by disturbance to a colony is an auditory warning from a conspecific, after which each individual's decision to remain or flee is virtually immediate. Males in the focal colony were more likely to flee the louder (higher the maximum amplitude) and noisier (higher the Wiener entropy) the conspecific vocalization that immediately preceded a disturbance event. Although the production and function of warning calls is well known, in weavers and in many other group-living animals, the result that has not, to our knowledge, been shown before is a graded response to continuous features of such a signal. The effect of higher amplitude could simply mean that more members of the colony heard the signal, especially since the colony itself was loud and situated alongside the Awash River. The independent effect of Wiener entropy, however, suggests an adjustment of the decision to flee based on a feature that is already known to be typical of alarm and warning calls (Collias 1963, 2000; Collias and Collias 2004). Whether weavers, or any other animals, give calls that vary in harshness or noisiness according to the level of threat is unknown. We hypothesize that they might do so, and that conspecifics can thus use these quantitative features to gauge the degree of threat and perhaps increase the effectiveness of their decision to flee or remain in the colony.

Once away from the colony, weavers face the decision of when to return. As predicted, they do not use features of the original alarm call (as they are now able to judge the safety of the colony visually from a distance); rather, they vary their order of return according to how many females reside on their territories and whether a nest is under construction. This finding is understandable in the light of previous research showing that nest materials are important commodities in a village weaver colony, and that males stand to lose materials by theft (Roulin 1999; Khan and Lahti in review), especially when construction is in progress (Crook 1963), and when the owners are away from their territories (Collias and Collias 1970, 1984; Din 1992). Thus, we propose that males incorporate this cost into their decision of how soon to return to the colony following a disturbance.

The findings of our study suggest 3 possible interpretations, which are not mutually exclusive. First, males might have different life-history strategies that explain both their mating status and their fleeing behavior: males might be situated on a continuum from a "live cautiously, die old" strategy, where they attempt to attract a few females and flee more readily, to a "live hard, die young" strategy, where they attempt to attract many females but take more individual risks, fleeing infrequently and returning soon (Ricklefs 1977; Zuk 1990). A second possibility is that males vary in risk-taking behavior and that females choose them on this basis, perhaps because they are more effective protectors of their territories. Thus, female choice would result in the observed association between the number of mates a male has and both his tendency to flee and his order of return. Thirdly, males might adjust their risk-taking behavior according to the value of their territory in reproductive

terms, i.e. how many breeding females reside on it. Males might take greater individual risks to protect their territory the greater the current value of that territory.

All 3 of the aforementioned factors could have played a role in the observed effects, but our data allow us to distinguish among the alternatives to some extent. The first hypothesis (variation among males in life-history strategy) and the second hypothesis (female choice for risk-taking males) both predict consistent male behavior independent of number of current mates. The third hypothesis (male adjustment of risk-taking according to reproductive value of the territory), however, predicts that a male adjusts his fleeing and returning behavior according to how many females reside on his territory. During our period of observation, the number of mates changed for all focal males except one, and every male engaged in riskier behavior when his number of mates increased, by fleeing less often. Thus, the most parsimonious explanation for variation among males in response to a colony disturbance appears to be that males are performing a cost-benefit analysis in real time, with the protection of one's territory trading off with self-protection. As more females inhabit the territory, the balance shifts towards more risk-taking behavior in service of the reproductive attempt.

These findings are compatible with other studies that have demonstrated that individuals have the capacity to mediate the tradeoffs associated with benefits and costs of taking risks. For example, Ghaleb and Martin (2002) found that hole-nesting bird species tend to reduce their individual visitation rates to the nest based on predation risk. Similarly, Fontaine and Martin (2006), in a study of several passerine species, revealed that individual females modulate their egg size, clutch mass, and rate of feeding based on experimental manipulation of predation risk. Hasselquist and Bensch (1991), in a mate-guarding study, reported relatively longer periods of vigilance in male reed warblers (*Arcocephalus arundinaceus*) when there was a reduced probability of attracting an additional mate and when there was a high risk of cuckoldry. Such studies provide evidence that risk-taking behavior is not necessarily a fixed trait but is the outcome of a real-time assessment of factors involved in fitness tradeoffs (Houston and MacNamara 1999). In fact, animals appear to perform these sorts of assessments regularly in a variety of situations (Stearns 1992; Gotthard and Nylin 1995; Lima 2009), the realization of which was a major impetus to the development of life history theory and the appreciation of adaptive plasticity in the late twentieth century.

Besides the alternative hypotheses of life history variation among males and sexual selection by females, age and colony size are 2 other potentially important causal factors in weaver risk-taking. We did find substantial variation in our data attributable to individuals (via male ID as a random effect), although we cannot determine whether these are effects of age or other differences among males. A longitudinal study of weavers breeding in aviary colonies revealed substantial variation in reproductive success among adult males, with no consistent relationship between age and annual reproductive success (Collias et al. 1986). Studies of weaver colonies of a variety of sizes would be useful in determining the extent to which colony size influences vigilance or individual risk-taking.

Studies of risk-taking behavior are almost always performed under artificial conditions (Toms et al. 2010; Beckman and Biro 2013; Carter et al. 2013). Such studies allow for controlled conditions and manipulations that are essential to understanding causation and mechanisms of behavior. Nevertheless, our purely observational study in the wild yielded results that account for important variation in natural behavior, including 2 results that we

believe are unprecedented, in this or any other species: that males respond in a graded fashion to warning calls, and that they are less likely to abandon their posts and quicker to return to them if they have more to lose on their territories in terms of females and nests.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Habig, Chiyo, and Lahti (2016).

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