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SHORT NOTE

Heterospecific intrusions, synchronous fleeing, and nest attendance in a weaverbird colony

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Abstract Synchronous fleeing (i.e. "dreads" or "panic flights") is a frequently observed but rarely quantified behaviour in colonial birds. Here we analyse video recordings to assess synchronous fleeing behaviour in a Village Weaver (*Ploceus cucullatus*) colony. Our results indicate that intrusions by heterospecific avian species are frequent and create significant daily differences in female nest attendance. Overall, different sizes, masses and species of intruding heterospecifics appear to affect weaver nesting similarly. Our findings suggest that in colonial birds, with the advantage of "many eyes", a rapid response to a potential threat nevertheless comes at the apparent cost of many "false alarms".

Keywords Behaviour · Fleeing · Panic flights · Nest attendance · *Ploceus cucullatus* · Weaver

Zusammenfassung

Fremdartige Eindringlinge, synchrone Flucht und Nestbewachung in einer Kolonie Webervögel

Die synchrone Flucht (auch „Panikflug") ist eine häufig beobachtete aber selten quantifizierte Verhaltensweise von Koloniebrütern. In dieser Studie analysierten wir Videoaufnahmen, um das synchrone Fluchtverhalten in einer Kolonie Dorfweber (*Ploceus cucullatus*) zu untersuchen. Es zeigte sich, dass Störungen durch fremdartige Vögel häufig waren und diese signifikante Unterschiede in der täglichen Nestbewachung durch Weibchen zur Folge hatten. Insgesamt schienen alle fremdartigen Eindringlinge einen ähnlichen Effekt auf die Dorfweber zu haben, unabhängig von deren Größe, Masse oder Artzugehörigkeit. Diese Ergebnisse verdeutlichen, dass eine schnelle Reaktion auf mögliche Gefahren in Koloniebrütern durch den Vorteil der „vielen Augen"dennoch den Nachteil vieler Fehlalarme mit sich bringt.

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Introduction

James Chapin first noted a striking phenomenon at Village Weaver (*Ploceus cucullatus*) colonies: "Suddenly an unwonted sight or noise alarms the birds; with one accord they dive obliquely from the tree and depart silently in all directions. Perfect quiet reigns, but not for long." (Chapin 1954: 353). In the decades following this observation, subsequent studies on other bird species (e.g. terns and gulls) have termed these synchronous flights "dreads" or "panic flights", and such behaviours have been reported to serve as anti-predatory defences (e.g. Marples and Marples 1934; Palmer 1941; Emlen et al. 1966). More recently, a number of studies (reviewed in Lima and Dill 1990) have investigated the interruption and resumption of feeding following a predatory intrusion. Although synchronous fleeing is striking in *Ploceus* weaver colonies, it has not

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been thoroughly described. Furthermore, the perceived risks that trigger these episodes are unknown. In the present study, we report a detailed observation of the phenomenon of synchronous fleeing in a Village Weaver colony and quantify its effect on female nest attendance.

Village Weavers have a polygynous mating system in which males vociferously compete with each other to establish and defend nesting space within the broader breeding colony (Collias and Collias 1970). An individual male can build and maintain five or more nests (Crook 1960). When females begin incubating eggs, male weavers defend their existing nests and continue to build and display at new ones. Males are largely uninvolved in parental care, and contribute mainly with vigilance at the nest (Collias and Collias 1970). Thus, weavers are simultaneously territorial and colonial—a breeding territory being composed of an aggregation of nests built by the same male, within the broader colony. As with most colonial species, this aggregation of displaying males increases the risk of attracting predators (Lima 2009). To counter this risk, the territorial and colonial behaviours displayed by weavers serve anti-predator functions—namely, the protective effects of mobbing, satiation, and dilution (Lima 2009). Furthermore, owing to the "many eyes" effect (Powell 1974), vigilance at breeding sites can generate an effective alarm system that is advantageous to indidviduals in the colony.

In this study, we determined whether time spent away from the nest following a synchronous fleeing event affects nesting bout length and daily nest attendance. If the cumulative effect of such disturbances is high enough, then females will show lower nest attendance on days with a greater number of synchronous fleeing events. Alternatively, time spent away due to fleeing events might be compensated by increasing attendance following the disturbances. We also identified heterospecific avian species that visited the colony, tested whether intruder size or species differentially affect nest attendance, and compared intrusions by known predators versus presumed non-predatory heterospecifics. Females might be able to distinguish predatory from non-predatory birds. Absent such discrimination, females might flee their colonies more readily in response to heterospecifics that are similar in appearance and size to known predators.

Methods

Please see the Electronic supplementary material (ESM) for detailed methods.

A Village Weaver breeding colony in Awash National Park in Ethiopia was observed during July and August 2010. A Canon VIXIA HF S21 camcorder was used to create video recordings of 30 focal females over a 6-day period (13 h of recordings encompassing all daylight hours). During video observation, we noted all instances of a *synchronous fleeing event* (an instance in which at least 75 % of the visible weavers fled the colony simultaneously). We recorded the *median duration of absence* for each fleeing event (the amount of time between synchronous flight and the point at which half the number of birds that fled returned to the colony).

We tested for correlations (Pearson) between (i) the total time that the colony experienced a fleeing event and the mean daily nest attendance, and (ii) nest attendance and time spent away from the nest due to synchronous fleeing events. We used a *t* test to compare the nest attendance of each female on the three days with the most fleeing events to her attendance on the three days with the fewest. We repeated the *t* test, excluding on and off bouts during and immediately after any synchronous fleeing event, to test whether females compensate for lost nesting time by increasing subsequent nesting bout length.

During video observations, we identified all heterospecific birds that entered the field of view and estimated their length (Redman et al. 2009) and mass (Dunning 2008). A Kruskal–Wallis rank sum test (KW) was applied to assess the probability that a female weaver would remain in the nest during intrusions by different species of birds. A generalized linear mixed effects model (GLMM) was used to assess the association between synchronous fleeing and (i) intruding species identity, (ii) duration of intrusion, (iii) species size (typical length and mass), (iv) territory size, and (v) temperature.

Results

A total of 36 synchronous fleeing events occurred during the 13 h of recording. The mean proportion of time that the weavers spent away from the colony following a fleeing event was 6.8 % (SD = 7.9), and ranged from 0 to 18 % on different days. A colony-level analysis revealed that, across days, the proportion of time spent away from the colony was negatively correlated with mean daily nesting bout length ($n = 6$, Pearson $r = -0.82$, $p = 0.048$). Daily nest attendance showed a similar trend, though it did not reach statistical significance ($n = 6$, Pearson $r = -0.71$, $p = 0.12$). Individual analyses showed that nest attendance was significantly lower on the three days with the highest number of fleeing events per hour, total number of fleeing events, and median duration of absence compared to the three days with the lowest values of these measures (*t* test: $t = 3.60$, $n = 14$, $p = 0.003$; Fig. 1a). When on or off bouts during and immediately following a synchronous fleeing event were excluded, the individual proportion of

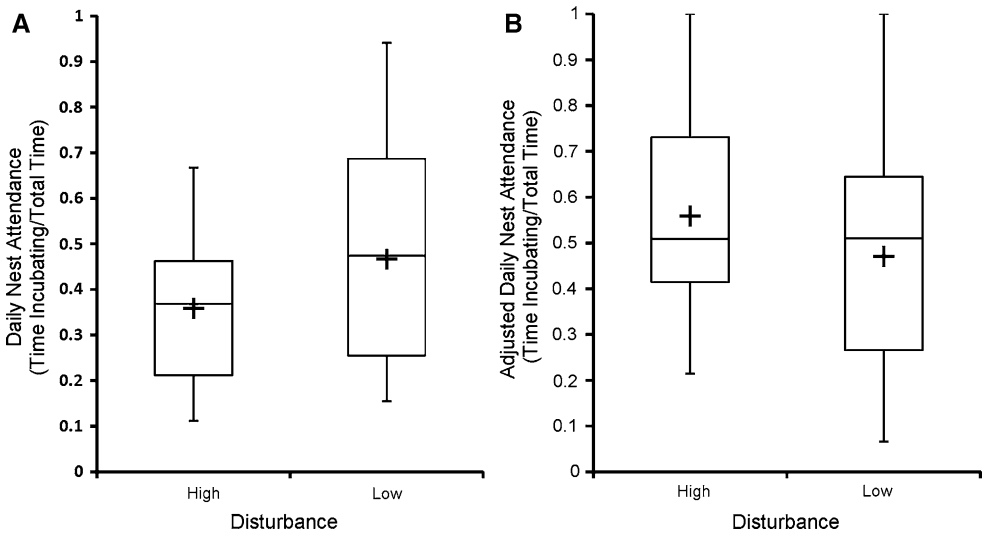

Fig. 1 Village Weaver nest attendance is affected by heterospecific intruders, but effects do not extend beyond the current nesting bout. **a** The mean proportion of nest attendance of female weavers was significantly lower on the three days with the highest number of fleeing events per hour, total fleeing events, and median duration of absence compared to the three days with the lowest levels of these measures of disturbance (*t* test: $n = 14$, $p = 0.003$). **b** However, this comparison was no longer significant after excluding the bouts (whether nesting or away) during and immediately after the synchronous fleeing event (*t* test: $n = 14$, $p = 0.59$)

Table 1 Bird species that intruded into an Ethiopian colony of Village Weavers (*Ploceus cucullatus*) during 13 h of video-recording over 6 days in August 2010

Species[a]	Body mass (g)[b]	Body length (cm)[c]	Number of visits	Duration of stay (s)[d]
Abdim's Stork (*Ciconia abdimii*)	1,398	81	1	0.3
African Gray Hornbill (*Tockus nasutus*)	163	51	8	0.5 (0.1–1.0)
Ethiopian Swallow (*Hirundo aethiopica*)	13.3	14	2	0.5 (0.2–0.7)
Eastern Gray Plantain Eater (*Crinifer zonurus*)	527	50	8	1.1 (0.1–3.6)
Gray-Headed Kingfisher (*Halycon leucocephala*)	41.8	21	3	0.5 (0.1–0. 8)
Hadada Ibis (*Bostrychia hagedash*)	1,238	75	2	272.8 (0.7–272.8)
Little Sparrowhawk (*Accipiter minullus*)[e]	84.1	23	3	13.8 (1.1–36.4)
Malachite Kingfisher (*Alcedo cristata*)	15.7	12	1	0.6
Spur-Winged Goose (*Plectopterus gambensis*)	3,869	100	1	0.6
Spur-Winged Plover (*Vanellus crassirostris*)	170	28	5	0.5 (0.2–0.8)
Striated Heron (*Butorides striata*)	187.5	40	22	0.4 (0.1–0.8)
White-Bellied Go-Away-Bird (*Corythaixoides leucogaster*)	220.8	50	4	0.7 (0.3–0.8)
Woodland Kingfisher (*Halcyon senegalensis*)	74.5	22	9	0.4 (0.1–1.1)

[a] Intruders in a further 11 cases could not be identified to species

[b] From Dunning (2008)

[c] From Redman et al. (2009)

[d] Mean (range, i.e. minimum to maximum)

[e] Predatory species

nest attendance no longer differed significantly between the three days with the highest levels of disturbance and the three days with the lowest level of disturbance ($t = 0.47$, $n = 14$, ns; Fig. 1b).

We documented 80 heterospecific intrusions at a rate of 6.15 per hour (SD = 5.69). We identified the intruder in 69 of these cases to 13 species (Table 1). Of these intrusions, three were by a predatory species, a Little Sparrowhawk (*Accipiter minullus*), and occurred on the same day. Typical intruder length ranged from 12 to 100 cm and intruder mass between 13 and 1,398 g. The average duration of an intrusion was 5.21 s (SD = 33.48), and ranged from 0.1 s to 4 min 33 s. The probability that females would remain on the nest during a heterospecific intrusion was not affected by the duration of the

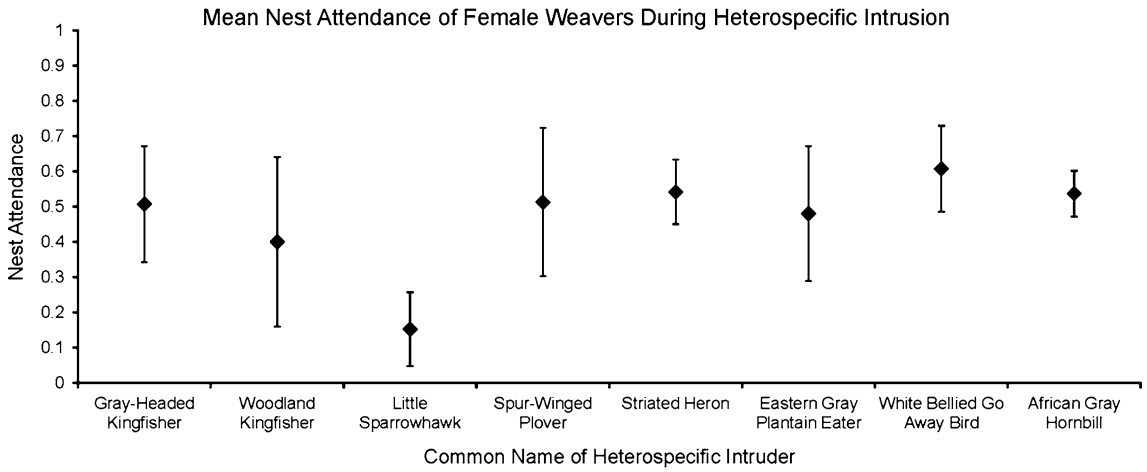

Fig. 2 Probability of nest attendance (with SD) of female Village Weavers during intrusion by heterospecific birds that entered the colony at least three times, arranged by body length. In a predator versus non-predator analysis, the Little Sparrowhawk (the only predator species) was associated with a significantly lower nesting probability than the nonpredators (Kruskal–Wallis: $\chi^2 = 7.33$; d$f = 2$; $p = 0.02$)

intrusion, the size of the intruding bird (both length and mass), temperature, or territory size (GLMM: $n = 1{,}301$; ns).

Female weavers had a lower probability of nest attendance during intrusions by a predatory heterospecific (three instances; same species) compared to intrusions by non-predatory heterospecifics observed at least three times (KW: $\chi^2 = 7.33$; d$f = 2$; $p = 0.02$; Fig. 2). This result was confirmed with a GLMM, which showed that the probability of female nest attendance was significantly higher during visits by non-predatory species than during visits by the predatory heterospecific (Table S1 of the ESM). When the predatory species was excluded from the analysis, the probability of female nest attendance during a disturbance did not vary significantly according to the species of intruding bird (KW: $\chi^2 = 7.90$; d$f = 7$; ns).

Discussion

Female Village Weavers in this Ethiopian colony were often interrupted by intrusions by other birds, and these interruptions were associated with synchronous fleeing events. Synchronous fleeing events reduced both nest attendance and mean daily nesting bout length. However, after the interrupted nesting bout, nest attendance returned to normal. Females did not adjust their nest attendance to counter the extent of interruptions, and so did not compensate for lost nesting time. Village Weavers did not adjust their response to different sizes and species of heterospecifics that intruded into the colony, except for the possibility—suggested by three episodes during our recordings—that they responded differently to a predatory bird. Thus, our results indicate that the advantage of a colony—the ability to respond to a threat quickly because of "many eyes"—can come at the apparent cost of many "false alarms" (Beauchamp 2010).

The high incidence of these false alarms, together with the equivalence of the responses to different intruders, begs explanation. Why, especially given the high frequency of nesting interruptions, were weavers not more tolerant of nonpredatory intruders? We present two non-mutually exclusive hypotheses. The first is that since predation events by birds involve rapid actions by predators, weavers can only avoid predation effectively if they rely on immediate response to collective detection (Fernández-Juricic et al. 2009), without pausing to corroborate by seeing or identifying the intruder. In fact, this mechanism relates to a strong candidate for the main function of colonial breeding, in weavers as in many other birds: individuals might benefit from breeding in colonies because more eyes can perceive predators more quickly, and they can copy each other in fleeing (Powell 1974). Such an instantaneous reaction is susceptible to false alarms, but might be less costly than any alternative behaviour given the circumstances. A second reason why weavers might flee from various intruding birds is that some birds that are not generally predators do occasionally prey on nests, including weaver nests. For instance, frugivores and insectivores have been observed preying on Village Weaver nests (Baker and Allen 1978; Wiley 2001; Lahti et al. 2002). Even if such intruders only attack eggs or young and not adults, a female weaver could be injured or killed if she remained in her nest during a nest predation attempt.

In one apparently typical and remote Village Weaver colony, disturbances to breeding were common enough, and their effects were extensive enough, to cause significant daily variations in synchronous fleeing events and nest

attendance. Variation in nest attendance occurred despite the fact that nearly all intrusions were by birds that are not regular predators. Moreover, females do not increase nest attendance following disturbances to compensate for interruptions. Perhaps such interruptions do not hinder egg development in a tropical environment, or else females sacrifice nest attendance rather than their own foraging when they lose time by fleeing. These hypotheses could be distinguished by monitoring the dynamics of incubation and by conducting experimental intrusions that keep females away from their nests for longer periods of time. Future studies should also assess variation in colony size and its effect on synchronous fleeing. Whereas the cost of fleeing is unclear, the benefit is easy to surmise. Escaping the colony upon the sudden appearance of an intruder, despite the high incidence of false alarms and the vulnerability of eggs or nestlings, might save the life of a female in the event of an attack on her or her nest.

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