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## **Costs and benefits in extreme nesting associations: do sociable weavers benefit from hosting African pygmy falcons?**

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### **Conflict of interest**

There are no conflicts of interest in this research.

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Avian nesting associations are a prominent feature of breeding bird communities. Protective associations between a predator and prey species represent a scenario where typically antagonistic interacting species may confer benefits to each species. The outcomes of these interactions are likely to be context-dependent and influenced by biotic and abiotic conditions. African Pygmy Falcons (*Polihierax semitorquatus*) are obligate nest associates of Sociable Weavers (*Philetairus socius*), using weaver colonies to breed and roost. As a result, the escalated rate of biotic interactions between associates may enhance rates of adaptation, speciation, and coevolution. Falcons occasionally prey on weavers but have the potential to defend colonies from nest predators. We used observational and experimental tests to determine if falcons deter snakes from accessing weaver colonies and if this increased nest survival for weavers that ‘host’ falcons in their colonies. We observed a reduction in the number of snakes at colonies hosting falcons and an increase in all colonies when weavers were breeding. Falcons were also more aggressive towards a snake stimulus than a control but only when they were breeding. However, weaver nest survival did not increase at colonies hosting falcons. Falcon defence likely reduces weaver nest predation by snakes; however, this is likely offset by nest predation by falcons. Additionally, we compared the breeding success of falcons whose breeding attempts overlapped with weaver breeding to those that did not. Weaver breeding did not explain falcon breeding success but did lead to an increase in falcon nest predation by snakes, and the likelihood that all chicks from a successful brood fledged, suggesting an ‘all or nothing’ scenario when weavers are breeding. In conclusion we show that both weavers and falcons incur costs and benefits of their close association (i.e., snake predation or food availability) and the net effects are likely to depend on the exact conditions in a particular breeding season. The intricacies of communalistic relationships continue to evade objective testing, and long-term demographic monitoring may offer better proof of the net benefits for each species.

## Introduction

Protective associations between a predator and prey species are ecological relationships where normally antagonistic interacting species may confer benefits to each other (Quinn and Ueta,

2008). This phenomenon is often described in avian systems, where timid species actively choose to nest near aggressive species that form a ‘protective umbrella’ around their own nest by excluding mutual predators (Bogliani *et al.* 1999, Sergio and Bogliani, 2001). Often the species providing protection is a potential predator of the protected associate or could cause reproductive failure (Burger, 1984, Bogliani *et al.*, 1999, Quinn and Kokorev, 2002). However, despite this threat, the protected species actively chooses to breed close to these potential predators (Norrdahl *et al.* 1995, Bogliani *et al.* 1999, Thomson *et al.* 2006, Mönkkönen *et al.* 2007), a decision which may ultimately enhance their mean reproductive success (Bogliani *et al.* 1999, Sergio and Bogliani 2001). The benefits gained through these interactions may be context dependent on prevailing environmental conditions, for example, nest predation pressure (Götmark 1989, Larsen & Grundetjern 1997). However, the interplay between these costs and benefits has not been quantified.

For the protector species, there are potential cost and benefits of having associations with timid species (Quinn and Ueta, 2008). Protector species may gain access to food by preying on nesting associate chicks or eggs (Norrdahl *et al.* 1995, Young and Titman, 1986). However, individuals or species nesting nearby may attract more predators, resulting in increased defence costs (Groom 1992), and an increased likelihood of having their own nesting attempts or even themselves succumb to predation. Nonetheless, of the studies that have investigated the costs and benefits to protective species (Wiklund 1979, Groom 1992, Larsen & Moldsvor 1992, Lindell 1996, Olson *et al.* 2001, Beier & Tungbani 2006), only Wiklund (1979) revealed any benefits. Specifically, he found that Merlins (*Falco columbarius*) provide protection for Fieldfares (*Turdus pilaris*), an already aggressive passerine, and when both species nest together they both gain greater reproductive success than non-associated pairs (Wiklund 1979, 1982). However, rarely do protective associates actively choose to nest near a timid species (Quinn and Ueta, 2008).

Here, we test the nature of the interaction between two species in an unconventional nesting association. Our study system involves an obligate nesting associate, the Pygmy Falcon (*Polihierax semitorquatus*; henceforth “falcons”) and its nest-building host, the Sociable Weaver (*Philetairus socius*; henceforth: “weavers”). Weavers build massive nest colonies that provide multiple resources for multiple species, and as such increase local activity and create biodiversity hotspots (Lowney & Thomson 2021, 2022). In southern Africa, falcons breed and roost exclusively within Sociable Weaver colonies (Oschadleus 2022), and both species utilize these structures year-round, benefiting from the temperature buffering that the insulated nest

mass provides (Lowney *et al.* 2020a). As a result, the escalated rate of biotic interactions between associates may enhance rates of adaptation, speciation, and coevolution (Schemske *et al.* 2009). Extreme systems, where species coexist in such proximity are ideal for gaining a greater understanding of close associations and determining how these may evolve (Lowney *et al.* 2020b).

Providing quantitative measures of success in an extreme avian nesting association provides insight into the evolution of these interactions. To date, the benefits and costs to weavers and falcons in this association have relied on anecdotal observations at colonies (Maclean 1970, Spiby 2014). We explore the reproductive outcomes of both species under different contexts and tested the mechanisms that allow these species to coexist simultaneously in nest colonies. Weavers appear to resent the falcons and instantly alarm when falcons are visible and disperse 87% of the time when falcons approach (Lowney *et al.* 2020b). The main diet of the falcon consists of reptiles and insects, and they also prey on small birds including Sociable Weaver adults and chicks, but to what extent is unknown (Maclean 1970, Covas *et al.* 2004, Spiby 2014). Falcons have been recorded killing conspecifics in territorial disputes (Lowney *et al.* 2017), therefore falcons are likely to be aggressive towards heterospecifics that pose a threat to their reproductive success. Maclean (1970) stated that he never observed snakes in colonies that host falcons and that he found no evidence that falcon breeding attempts were predated by snakes. This is extraordinary considering up to 70% of weaver breeding attempts are predated; mainly by snakes (Maclean 1973a, Covas *et al.* 2004, Pacquet *et al.* 2015).

We investigated the association between weavers and falcons to identify distinct association benefits. Firstly, we focused on whether falcons can defend colonies from predators, particularly snakes. Our responses compared the reactions of falcons to snake and control stimuli. We also compared the likelihood that snakes are observed at colonies that host falcons with those that do not. We hypothesized that falcons will aggressively defend against a snake stimulus and that there will be a reduction in the number of snakes seen at these colonies. Secondly, we compared the nest predation rates of weavers breeding at colonies that host falcons compared to those that do not. We hypothesized that if falcons aggressively defend colonies against snakes, this will reduce nest predation rates of weavers breeding in colonies that host falcons. Thirdly, we explored the potential breeding costs and benefits to falcons when breeding concurrently with weavers. Here, we hypothesized that falcon breeding success may increase when weavers are breeding due to the increase in weaver chicks as available food

resources. Alternatively, an increase in snake activity at colonies when weavers are breeding may see a reduction in falcon breeding success, even if they act aggressively towards predators.

## METHODS

### Study site and data collection

This study was carried out at Tswalu Kalahari, a reserve in the Northern Cape, South Africa (27°13'30"S and 22°28'40"E). Our main study area consists of 130 km<sup>2</sup> containing over 250 weaver colonies, mostly in the two dominant tree species: camelthorn *Vachellia erioloba* and shepherds tree *Boscia albitrunca*. Annually, there are between 29 and 39 active falcon territories in the study area and each territory can contain 2-5 adult birds (Bolopo *et al.* 2019). Falcon territories can contain multiple weaver colonies, but falcons only occupy one (rarely two) weaver colonies at a time, preferring the larger colonies (Olubodun *et al.* 2023). Falcon groups and territories have been observed since 2011, with all adults being colour-ringed from 2015 onwards (Bolopo *et al.* 2019). The data for this study was collected during three breeding seasons (late 2015 to early 2018).

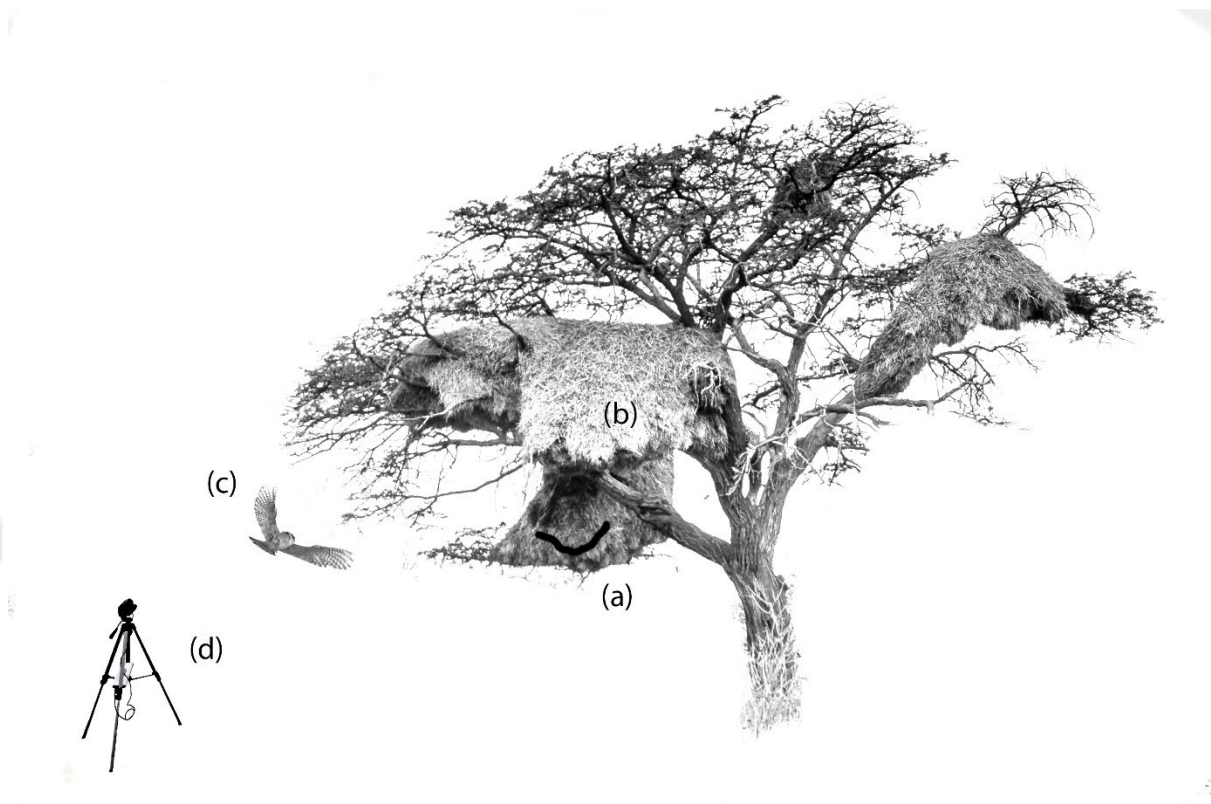
Weaver colonies are a large nest mass (sometimes up to four nest masses in a single tree) made up of multiple individual nest chambers. In the study area, these colonies range in size between 2 – 238 nest chambers. Weaver breeding is highly influenced by rainfall. In years with higher rainfall weavers have longer breeding seasons, more clutches and larger clutch sizes. Weavers have been recorded laying up to nine clutches in a breeding season following successive nest predation events (Covas 2002). Clutch size tends to vary between 2-6 eggs (Mendelson & Anderson 1997).

### Pygmy Falcon reaction to model predators

To understand how falcons potentially respond to predators at weaver colonies we conducted a simple experiment. We fixed plastic toy snakes (treatment) or a ball (control) to colonies that hosted falcons. We conducted the experiment at twelve different colonies that contained falcon nests with three-week-old chicks (see below). We used two different model snakes, each at six colonies. They were 46 cm long and 2 cm diameter. A small soft football was used as the control (8cm) diameter. The order of presentation between the snake and the control changed between each experiment. Stimuli were attached to colonies using plastic wire ties. To prevent habituation, the second stimulus was presented three days after the first.

The stimulus was attached to a colony when at least one of the breeding adults was present and a video camera (Legria HF R 606) filmed any response for 45 minutes. The researcher left the area, eliminating any observer influence on falcon behaviour. The camera was mounted on a tripod with unobstructed views of the colony and stimulus (Figure 1). Data extracted from the videos were: 1) if falcons responded aggressively (yes/no), defined as a falcon mobbing the stimulus, and 2) the level of aggression defined by the number of times a falcon mobbed the stimulus.

These experiments were repeated using the same individual falcons (identified by their colour rings), three months later, when falcons had finished breeding. The falcons received the same decoy snake and presentation order as before. Two falcon groups were excluded because after breeding they had moved to a colony that was too high to attach the stimuli.



**Figure 1.** The experiment set-up. A snake stimulus (a) was attached to a colony (b) that hosted pygmy falcons (c). The researcher left the area while a video camera (d) filmed any response for 45 minutes, eliminating any observer influence on falcon behaviour.

### Snake encounter rates

To determine if falcon colony occupation influenced the likelihood of encountering snakes at a colony, we recorded snake presence at weaver colonies that hosted falcons and at paired

weaver colonies that did not. The number of colonies visited varied between years due to the fluctuation in the number of falcon territories; 36 colonies in 2015-2016 and 2016-2017, and 26 colonies in 2017-2018. Falcons have multiple colonies within a territory and can move between colonies from year to year. Therefore, a falcon-occupied colony paired with a control in one year may be paired with a different colony the following year potentially causing an unequal number of colonies observed despite the paired design. Paired colonies were on average 699 m apart ( $\pm 102$  m SE, range 58 – 2300 m; means  $\pm$  standard error unless otherwise stated) and were of similar size (mean 82 chambers  $\pm 4.37$ , range 12 - 238) and matched for tree species. We recorded colony height above ground and used the number of chambers as a proxy for colony size as these positively correlate with the size of the structure (Leighton & Echeverri 2014). We visited these colonies at least once every seven days during the peak breeding seasons (October – March) between 2015 and 2018, with paired colony trees being visited on the same day immediately after each other.

### **Weaver and falcon breeding success**

We inspected nest chambers of falcons and weavers in 48 unique colonies every 4-7 days throughout the breeding season to detect any initiated breeding attempt (i.e., the laying of clutches). Due to the size of many of our colonies, we monitored a subset of chambers per colony (mean 29, range 12 – 42), with the same number of chambers monitored at paired colonies. We focused on chambers in the centre of the colony structures as this is where most of the breeding occurs (Van Dijk *et al.* 2013). All falcon-occupied chambers were monitored because falcons mark their chambers with a conspicuous white faecal mat allowing easy chamber identification (Krochuk *et al.* 2018). Each chamber was inspected using a Rolson 60515 Two LED Telescopic Inspection Mirror.

Any weaver or falcon breeding attempts recorded were closely monitored to determine nest fate and reproductive output. To determine hatching dates, the frequency of nest visits increased near the estimated hatching date. Weaver nestlings fledge at 21-24 days old (Maclean 1973b); however, premature fledging may occur if disturbed from day 18 onwards. Therefore, the last time we checked a nest was when the oldest chick was around 17 days old. If the oldest chick survived to day 17 then we assumed that the brood fledged and recorded the nest as successful.



Falcon nests hatch after ~33 days of incubation and chicks remain in the nest for a further five weeks (Olubodun *et al.* 2023). From day 24, chicks are large enough to be seen by observers standing below the colonies without using the mirror, and if the chamber appeared empty, we would then scan the territory looking for fledged chicks. If only some of the chicks were seen, we would check colonies at night with a headlamp. We recorded how many chicks returned and this allowed us to determine the number of chicks that successfully fledged.

We classified the disappearance of nest contents as predated if the contents of two or more adjacent breeding chambers were also discovered empty (Covas *et al.* 2008). If falcons were breeding but weavers were not, then the nest predation of a falcon nest would be classified only when the full contents (all eggs or chicks) of a falcon nest disappeared. In addition, all chambers that were found empty the day after a snake was observed at a colony were also classified as predated (Covas *et al.* 2008).

### **Statistical analysis**

All data were analysed using R package 4.1.2 (R Core Team 2021). We used generalised linear mixed models (GLMM) to test all response variables using the lme4 package (Bates *et al.* 2015). Poisson or negative binomial (for over-dispersed data) distributions were used to analyse count data (O'Hara & Kotze 2010). Over dispersed data were calculated by dividing the residual degrees of freedom by the deviance. Initially, we entered “year” as an explanatory variable in models, however due to harsh environmental conditions in 2015 and 2017, the number of breeding attempts in those years were extremely limited meaning that “year” did not explain any variation affected our ability to undertake robust statistical tests, therefore we omitted the explanatory variable “year” (breeding season) from our models. We additionally used the number of chambers as an explanatory variable in all models testing breeding success, as colony size influences weaver breeding success (Covas 2002).

We examined falcon behaviour to simulated snake presence using falcon response to a model stimulus (yes/no) and the level of aggression (number of times the falcon mobbed the stimulus). These models with a binomial error and negative binomial distributions, respectively, included the explanatory variables, treatment (snake or control stimuli), the order of treatments (first or second) and the number of chicks that were in the nest. Group ID was used as a random effect to account for non-independence for the multiple trials a group experienced.

To determine if falcon colony occupation explained the probability of encountering a snake at a colony, we used the binomial response variable ‘snake presence’ (yes/no) and the explanatory terms were falcon occupation (yes/no), weavers breeding (yes/no), colony size (number of chambers) and colony height (cm above ground). Colony ID was nested within paired colonies ID as a random effect to account for non-independence for multiple nests monitored within the same colony and paired spatial dependence between paired colonies. To test if active falcon breeding explained the probability of snake encounters, we subset the data to only include colonies that hosted falcons and included the explanatory variable of falcons currently breeding (yes/no). Only Tree ID was used as a random effect.

We used logistic exposure models to estimate the daily probability of survival for weaver and falcon nesting attempts as this allowed for variation in the intervals between nest checks. Colony size and colony height were used as explanatory variables, and colony ID was used as a random term in all models. For tests where paired control trees were used, pair ID was also included as a random term with colony ID nested within pair ID. The number of days between each visit was used as an offset in these statistical tests. If a nest was discovered with at least one hatched chick and had not been observed during the egg stage we then allocated 15 days for the offset for weavers and 28 days for falcons as this was the average length of the egg stage in these species, respectively.

We carried out three different tests to determine if the falcon occupation of a colony affected weaver nest survival at different stages of the nesting period. We tested if the falcon colony occupation affected nest survival as a whole, during the egg stage, and during the chick stage. At times we were unable to determine the exact hatching dates due to nests hatching between visits. Therefore, when comparing egg survival rates, we used data from nests until the eggs either hatched or were predated. When comparing chick survival, we used data from the exact hatching date until either they had reached day 17 or had been predated. For those nests where we did not know the exact hatch date, we used the data from the last date they were observed as eggs. To examine how falcon breeding may explain weaver breeding success (same response variables as above), we subset the data to only use colonies that hosted falcons and included falcon breeding (eggs or chicks in the nest, yes/no).

Lastly, we examined if weaver breeding explained falcon nest survival, breeding success and the probability of falcon nests being predated. We used logistic exposure models to determine nest survival (see above) and used weaver breeding (yes/no) as an additional explanatory term.

We used binomial response variables, nest success (at least one chick fledged, yes/no), whether the full clutch fledged (yes/no), and the reason behind any nest failures; nest predated (yes/no) and nest failure due to reasons other than predation (yes/no). To determine the probability of a full clutch fledging, we subset the data and used only data from breeding attempts where at least one individual had fledged. We also compared the number of falcon chicks that successfully fledged, using an LLM. Explanatory variables used in the model were, weavers breeding (at least one active weaver nest in the colony, yes/no), colony size and colony height. We also used a binomial GLMM to determine the probability the successful nests fledged the full brood. Here we subset the data, using only data from breeding attempts where at least one individual fledged and used the weavers breeding, colony size and colony height as explanatory variables.

## Results

### Pygmy Falcon responses to model snakes

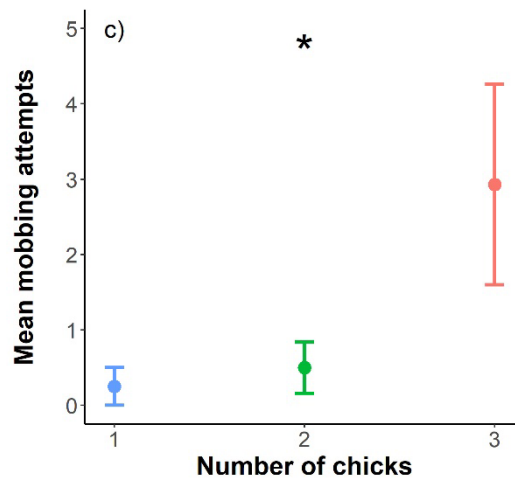
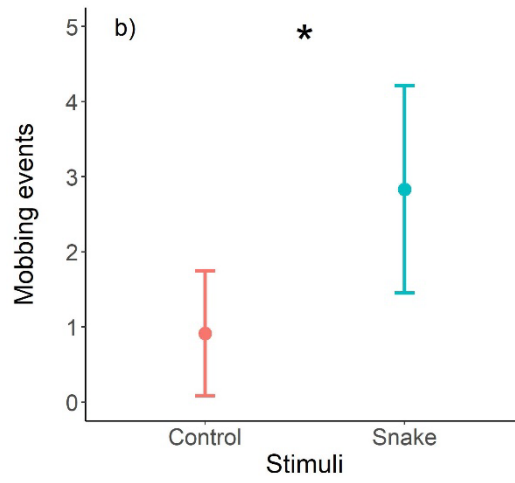
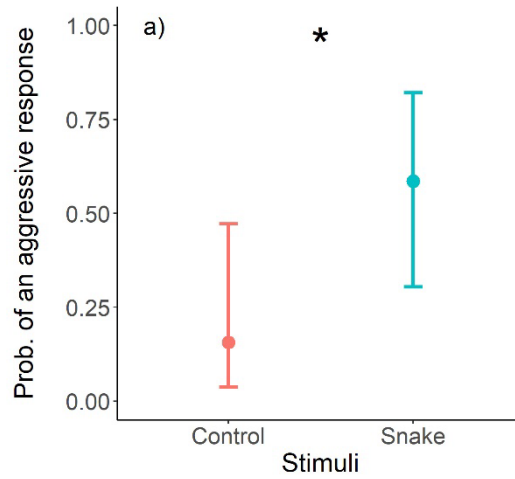
Falcons responded to stimuli during nine of 24 experimental trials when they were breeding, attacking the stimuli a total of 45 times (mean = 1.86; range 0 – 15). In contrast, falcons did not respond to stimuli at all when not breeding. Complete lack of response to either stimulus when falcons were not breeding precluded statistical analyses.

For experiments when falcons were breeding, stimulus type significantly explained the probability of aggressive falcon attacks (Table 1a). Falcons showed aggressive responses in 58% (7 of 12) of the trials when presented with a snake stimulus compared to 17% (2 of 12) when presented with the control stimulus (Figure 2a). When responding aggressively, falcons attacked the snake stimuli 34 times (mean 2.83 times  $\pm$  1.38) and the control only 11 times (0.92  $\pm$  0.83; Table 1b; Figure 2b) and would attack a given stimulus more often when they had more chicks to defend (Table 1b; Figure 2c).

**Table 1.** Results from the generalised linear mixed models investigating (a) the probability of an aggressive falcon response to the different stimuli placed at their breeding chambers, and (b) the level of aggression displayed. *Overdispersion parameter for the level of aggression (b) = 2.49*

Response variables	Explanatory variables	Estimate	$\pm$ SE	$\chi^2$	<i>P</i>
a) Aggression	Stimuli			4.09	0.04

n=24	Order of stimuli presentation			0.25	0.62
	Number of chicks	0.51	0.66	0.60	0.44
b) Level of aggression n=24	Stimuli			7.72	0.005
	Order of stimuli presentation			1.68	0.19
	Number of chicks	2.51	1.22	4.20	0.04



**Figure 2.** The probability (model predicted values  $\pm$  95% CI) of (a) falcons responding aggressively towards presented stimuli, (b) the mean number of times falcons physically attacked the stimuli, and (c) the mean number for times the falcons attacked a stimulus in response to the number of chicks inside the nest. (\* denotes  $p < 0.05$ , \*\* denotes  $p < 0.01$ ).

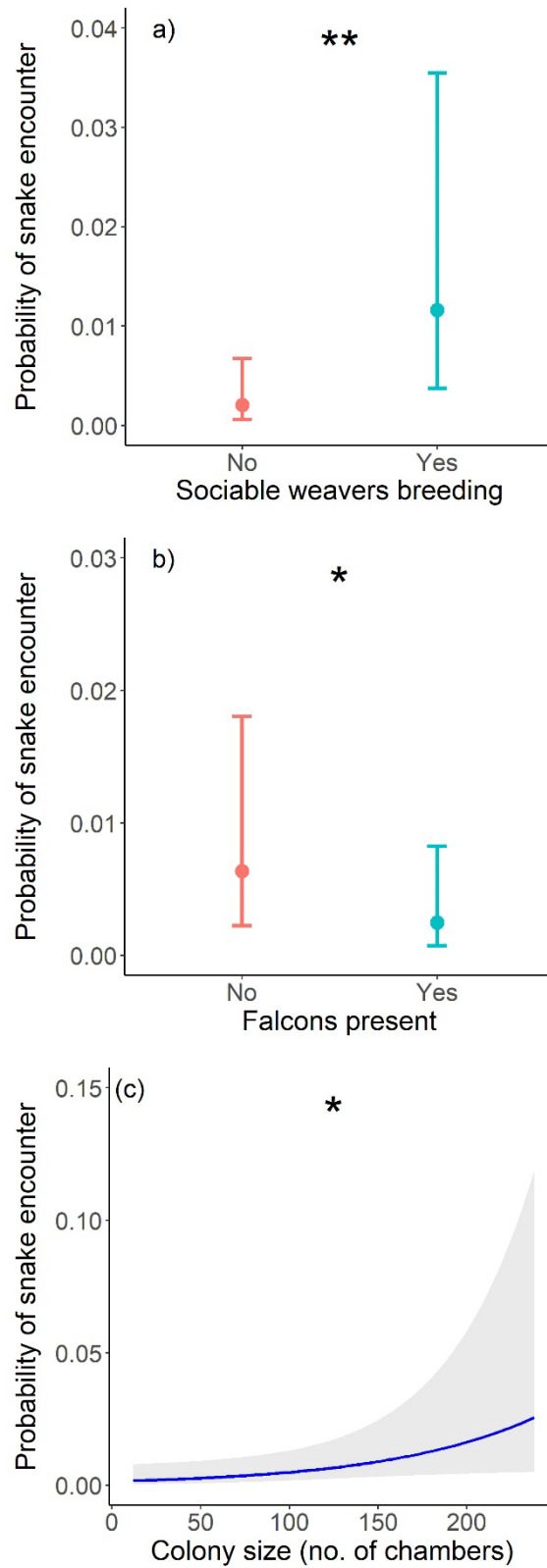
### Snake encounter rates

A total of 2090 visits to 48 unique colonies were carried out, with thirty-two snakes observed. Two species of snakes were recorded at weaver colonies, cape cobras (*Naja nivea*) on 26 occasions, and boomslang (*Dispholidus typus*) on six occasions.

The probability of encountering a snake at a colony was significantly explained by weaver breeding, falcon occupation of the colony and colony size (Table 2a). When weavers were breeding, snakes were encountered nearly seven times more frequently than when weavers were not breeding (1.6% vs 0.2% of colony visits, Figure 3a). With weaver breeding accounted for, colonies that hosted falcons had snakes on 0.4% of visits, which was less than half as often as encountering snakes at 1% of visits to colonies without falcons (Figure 3b). The probability of encountering snakes also increased at larger colonies from a predicted 0.1% at the smallest 12 chamber colony to a predicted 5% at the largest 238 chamber colony (Figure 3c) and colony size is therefore accounted for in all results. The probability of snake encounters was not significantly explained by active falcon breeding attempts, in a subset of colonies that all contained falcons (Table 2b).

**Table 2.** Results from the generalised linear mixed models investigating factors that may impact the probability of (a) snake encounters at all colonies and (b) for a subset of colonies hosting falcons.

Response variables	Explanatory variables	Estimate	$\pm$ SE	$\chi^2$	<i>P</i>
a) Snake encounters n=2090	Falcons present (Yes/No)			5.13	0.02
	Weavers breeding (Yes/No)			10.21	0.001
	Colony size	0.53	0.25	4.52	0.03
	Colony height	0.01	0.01	1.04	0.31
b) Snake encounters n=1034	Falcons breeding (Yes/No)			0.26	0.61
	Weavers breeding (Yes/No)			4.26	0.04
	Colony size	0.51	0.38	1.72	0.19
	Colony height	0.01	0.01	0.22	0.64



**Figure 3.** The probability of encountering snakes (model predicted values  $\pm$  95% CI) at Sociable Weaver colonies when (a) weavers are and are not breeding, (b) when pygmy falcons

are and are not present, and (c) in relation to colony size (\*\* denotes  $p < 0.01$ , \* denotes  $p < 0.05$ ).

### Sociable Weaver breeding success

In total, 825 weaver breeding attempts were monitored, (mean per colony  $19.18 \pm 1.8$ , range 1 – 45), of which 7% of all outcomes (122 out of 825) were unknown (mean per colony  $3.94 \pm 0.37$  SE). Of the remaining 703 attempts, 52% hatched (364 out of 703, mean per colony  $8.85 \pm 0.87$  SE), and 9% (64) were successful at fledging at least one chick (mean per colony  $2.91 \pm 0.49$ ). Overall, 62% (434) of weaver nests were predated (mean per colony  $10.08 \pm 1.02$  SE).

Falcon occupation of a colony did not explain the probability of overall nest survival (Table 3a) at any stage (Table 3b). To compare, 42% of clutches hatched (173 out of 408) at colonies hosting falcons, compared to 46% (190 out of 417) in colonies without falcons. For hatched nests only, falcon presence did not explain the probability of nests with chicks being predated: 21% (39 out of 190) of nests at colonies hosting falcons, compared to 14% (24 out of 173) in colonies without falcons (Table 3c). For the subset of colonies that hosted falcons, overall nest survival, survival of nests during the egg or chick phase were not explained by whether falcons were breeding or not (Table 4).

**Table 3.** Results of logistic regression models comparing weaver nest survival compared to whether falcons were or were not present in colonies; (a) overall nest survival, (b) egg survival, and (c) chick survival.

Response variables	Explanatory variables	Estimate	$\pm$ SE	$\chi^2$	<i>P</i>
a) Overall nest survival n=825	Falcons present (yes/no)			1.90	0.17
	Colony size	0.03	0.03	0.63	0.43
	Colony height	-0.02	0.03	0.40	0.53
b) Egg survival n=825	Falcons present (yes/no)			1.70	0.19
	Colony size	0.03	0.04	0.60	0.44
	Colony height	-0.05	0.04	1.35	0.24
c) Chick survival n=364	Falcons present (yes/no)			2.35	0.12
	Colony size	0.03	0.05	0.36	0.55
	Colony height	0.05	0.05	1.18	0.28

**Table 4.** Results from the logistic regression models comparing weaver nest survival at colonies hosting falcons. We compared weaver (a) overall nest survival, (b) egg survival, and (c) chick survival depending on whether falcons were or were not breeding.

Response variables	Explanatory variables	Estimate	± SE	$\chi^2$	<i>P</i>
a) Overall nest survival n=408	Falcons breeding (yes/no)			0.48	0.49
	Colony size	0.01	0.04	0.07	0.79
	Colony height	-0.002	0.04	0.002	0.96
b) Egg survival n=408	Falcons breeding (yes/no)			0.68	0.41
	Colony size	0.04	0.06	0.49	0.49
	Colony height	-0.03	0.05	0.28	0.60
c) Chick survival n=173	Falcons breeding (yes/no)			2.41	0.12
	Colony size	0.05	0.06	0.73	0.39
	Colony height	0.11	0.06	2.90	0.09

#### Pygmy Falcon breeding success

In total 57 falcon breeding attempts were monitored. Two attempts were abandoned, potentially due to human disturbance, and were subsequently removed from further analyses. In total, 51% (28 out of 55) successfully fledged at least one chick, while 20% (11 out of 55) were predated (all presumed to have been by snakes), and 30% (16 out of 55) failed due to reasons other than predation.

Weavers actively breeding at a colony during falcon breeding attempts did not explain the probability of falcon nest survival (Table 5a). Falcon breeding success was not explained by whether weavers were (9 of 23; prob.  $0.39 \pm 0.1$  SE) or were not breeding (19 of 32;  $0.60 \pm 0.9$ ; Table 5b). However, the probability of falcon nests being predated was six times greater when weavers were breeding (9 out of 23;  $0.40 \pm 0.1$ ) compared to when they were not (2 out of 32;  $0.06 \pm 0.04$ ; Figure 4, Table 5c). The probability of failure due to reasons other than predation was also not explained by weavers breeding (3 out of 23;  $0.32 \pm 1.0$ ) or not breeding (11 out of 32;  $0.15 \pm 0.9$ , Table 5d). On average,  $1.13 \pm 0.19$  and  $0.76 \pm 0.18$  falcon chicks fledge when falcon and weaver breeding do and do not overlap, respectively (Table 5e). Of the falcon broods that fledged when weavers were breeding, 8 out of 9 (90 prob.  $\pm 0.11$  se) fledged

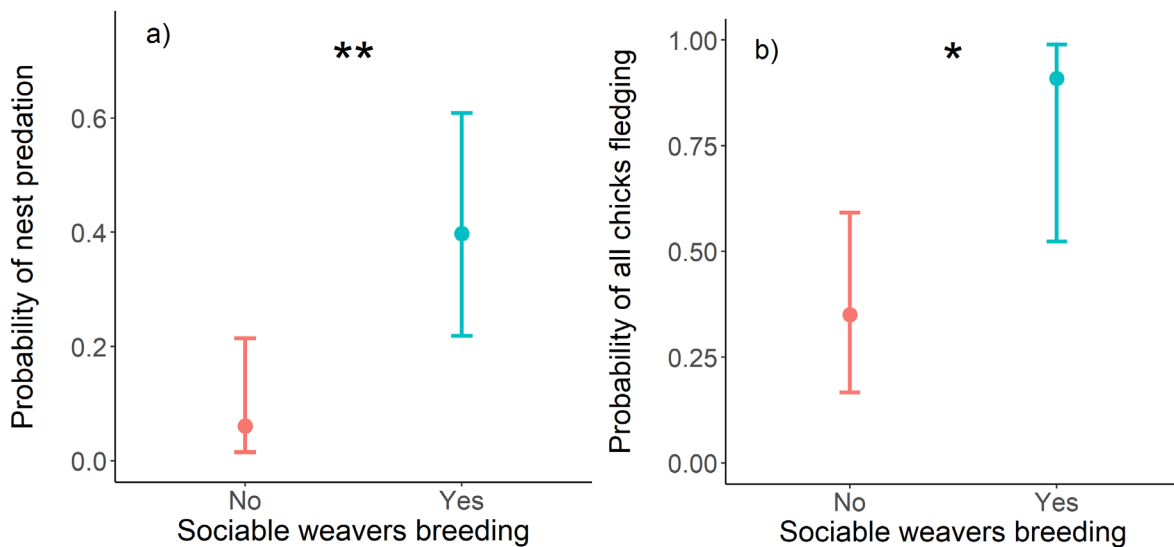


full broods, compared to 7 out of 19 ( $0.35 \pm 0.09$ ) when weavers were not breeding (Table 5f; figure 4b).

**Table 5.** Results from the generalised linear mixed models comparing falcon breeding success in colonies when weavers were and were not breeding. (a) logistic regression comparing falcon nest survival, (b) breeding success, (c) the likelihood of nest predation (d) the likelihood of nest failure due to reasons other than predation, (e) the average number of chicks that fledged and (f) of the broods that fledged the probability of all individuals fledging.

Response variables	Explanatory variables	Estimate	$\pm$ SE	$\chi^2$	<i>P</i>
a) Overall nest survival	Weavers breeding (yes/no)			3.41	0.06
n=55	Colony size	-0.169	0.130	1.70	0.19
	Colony height	-0.066	0.131	0.25	0.62
b) breeding success (yes/no)	Weavers breeding (yes/no)			2.14	0.14
n=55	Colony size	-0.058	0.295	0.04	0.84
	Colony height	-0.092	0.296	0.10	0.75
c) Probability of nest predation (yes/no)	Weavers breeding (yes/no)			7.21	0.007
n=55	Colony size	0.214	0.391	0.30	0.58
	Colony height	0.028	0.397	0.01	0.94
d) Nest failure, other than predation (yes/no)	Weavers breeding (yes/no)			3.03	0.08
n=55	Colony size	0.304	0.386	0.62	0.43
	Colony height	0.01	0.385	0.001	0.97

e) Number of Chicks fledged	Weavers breeding (yes/no)			1.73	0.19
n=55	Colony size	0.06	0.143	0.18	0.68
	Colony height	-0.04	0.146	0.07	0.78
f) Probability of the full clutch fledging	Weavers breeding (yes/no)			5.37	0.02
N = 28	Colony size	0.57	0.51	1.26	0.26
	Colony height	0.10	0.52	0.04	0.85



**Figure 4.** The probability of falcon breeding success (model predicted values  $\pm$  95% CI) when weavers are and are not breeding, (a) the probability of nests predation, and (b) of the broods that fledged the probability of all individuals fledging (\*\* denotes  $p < 0.01$ ).

## Discussion

Our study highlights that the interaction between sociable weavers and pygmy falcons is an interplay of costs and benefits to both species. We found that falcons provide protection against snake predation at weaver colonies, and that fewer snakes were encountered foraging at colonies that hosted falcons. However, weavers ‘hosting’ and coexisting with falcons in colonies did not show increased reproductive output. Indeed, our study suggests that the protection benefits provided by falcons to limit snake predation might be offset by nest

predation conducted by falcons on weaver nests. While falcons may forage on weaver chicks, the availability of this food resource is not reflected in a higher falcon reproductive output when weavers are breeding, potentially due to the higher likelihood of snake encounters (and subsequent nest predation on falcon nests) at colonies when weavers were breeding.

Falcons actively attempt to repel simulated snakes from foraging in weaver colonies. This matches our own direct observations of falcons attacking and deterring real snakes from accessing colonies. This aggressive defence only occurs when they were breeding, suggesting that any benefits that weavers may derive from falcons are limited to the period when falcons are breeding, which matches findings from other avian breeding associations (Ueta 1994, Ueta 2001, Bogliani *et al.* 1999). We also found evidence that falcons were more aggressive when they had more chicks to defend, supporting theory that as the reproductive value of the current reproductive event increases, investment in defence increases (Lima 2009). Despite this, we found that falcons nests were also predated by snakes, meaning that aggressive defence against these predators was not always successful. We have no evidence that falcon defence is a mortality risk for snakes, therefore snakes may attempt to access colonies despite falcon presence and can also do so at night when falcons are unable to defend their nests (Lowney *et al.* 2022). These findings highlight that understanding context-dependent variation in nest defence, and snake foraging is important to understand the outcomes in this association.

Weavers did not show reproductive output benefits from falcon 'protection'. Our results suggest snakes forage in colonies more often when weavers are breeding and when colonies are larger, although part of this signal might be explained by snakes spending longer in larger colonies. Interestingly, falcons also favour occupying bigger weaver colonies (Olubodun *et al.* 2023). Nevertheless, despite falcons being able to repel snakes from weaver colonies, we found that this did not lead to an increase in reproductive output for weavers. Overall, weaver nest success rates were extremely low (only 9% were successful), both in colonies that hosted falcons and those without falcons. Part of this might be driven by low rainfall in 2016 and 2018, however our methods of focusing on the more central chambers may have increased the overall survival rate due to those chambers on the edge likely being more susceptible to snake predation. Protective nesting associations in birds will never eliminate nest predation risk as shown in other systems (Bogliani *et al.* 1999) but these rates of nest success were lower than those reported elsewhere for the weavers, notably from an area with only rare falcon presence (Covas 2002, Pacquet *et al.* 2015).

Our results suggest that the nest predation pressure imposed by falcons (the “protector species”) on weavers is biologically meaningful and potentially additive. We were unable to distinguish between snake and falcon nest predation of weaver nests, however the probability of snakes foraging on weaver nests halved when falcons were breeding in a weaver nest. Therefore, similar predation rates of weaver nests that were documented with and without falcons, which actually tended towards higher nest predation rate with falcons present, suggests that the protective benefits provided by falcons on weaver nests is potentially fully offset by increased falcon nest predation in colonies occupied by falcons. Falcon predation on weaver chicks has been documented previously (Maclean 1970, Covas *et al.* 2004, Spiby 2014, personal observations) but suggested to be rare (Maclean 1970). However, we observed falcons searching weaver chambers on average once every *ca.* 2 hours when weavers were breeding, compared to once every *ca.* 20 hours when weavers were not (A. Lowney, unpublished data). While we found no clear net reproductive benefits/costs of this ‘enforced protective’ association, falcon colony occupation may further positively or negatively impact weaver fitness through impacts on adult survival for instance. Indeed, there may be individual falcon variation, which is relevant in these interactions, for example Bogliani *et al.* (1999) showed that certain Hobby Falcons were more aggressive than others and were more likely to successfully deter predators. In the current system, there may be individual variation in falcons propensity to defend aggressively and to predate weaver nests or indeed weaver adults, and this interaction needs to be further explored.

Pygmy Falcons gain benefits, from their reliance on weaver colonies, as they do not need to build their own nests, the nests are insulated from extreme external temperatures, and feed on weaver chicks, but we documented putative costs too. When falcon breeding overlapped with weaver breeding, falcon nests suffered higher nest predation rates due to the attraction of snakes to the weaver colonies. In these conditions falcons mostly either fledged all or none of their young, suggesting high food availability (weaver chicks), but also high nest predation rates (many snakes). Nevertheless, overall falcon reproductive output did not differ when weavers were and were not breeding. Falcons do not invest time or energy in building and maintaining nests and gain a nesting chamber that is buffered from temperature extremes (Lowney *et al.* 2020a). With a breeding cycle duration that is double the length of the weavers, falcons are unable to avoid overlap in breeding with weavers which could initiate breeding after falcons and overlap would still occur. Our findings highlight the costs that the protector ‘aggressive’ species may encounter in nesting associations, an aspect neglected from other studies (Quinn

& Ueta 2008). The falcon-weaver association is exceptional because the falcon depends on weaver colonies and may have adaptations to decrease these costs.

The interplay of costs and benefits between weavers and falcons may be important more broadly because weaver colonies are a crucial 'resource' to the Kalahari animal community, especially in harsher areas (Lowney & Thomson 2022). Sociable Weavers are ecosystem engineers, and their colonies are used by a wide range of animals (Maclean 1973 Lowney et al. 2020b, Lowney & Thomson 2021), impact soil nutrients, and the formation of islands of fertility in the landscape and vegetation growth (Prayag *et al.* 2020, Aikins *et al.* 2023a, 2023b). As predators, pygmy falcon occupation of colonies may also impact the occurrence of species that associate with weaver colonies (e.g., Rymer *et al.* 2014). Indeed, weavers have also been reported to occasionally abandon their colonies after falcons move in (Covas *et al.* 2004), suggesting high costs to weavers overall, and the importance of the falcons in this system.

Biotic and abiotic conditions may also affect the outcomes of nesting associate interactions (Götmark 1989, Larsen & Grundetjern 1997, Quinn & Ueta, 2008, Canestrari *et al.*, 2014). For example, the variable timing of breeding of the two species (Mares et al. 2017, Olubodun *et al.* 2023) holds significant consequences for the net fitness outcomes. Predation pressure will also alter the net outcomes; weaver nest predation pressure by snakes (and indeed falcons) may change due to environmental conditions, especially in arid environments where resource availability fluctuates between abundant and scarce (Hillel & Tadmor 1962, Rosenzweig 1968). In years of high nest predation pressure by snakes, there may be benefits for weavers to co-inhabit a colony with falcons, because snake visits are destructive and could predate every active nest in the colony (Covas 2002). Falcon populations also fluctuate between years (Bolopo *et al.* 2019, Olubodun *et al.* 2023), and an increased number of falcons in a landscape may increase competition for resources, adding to weaver predation pressure. These aspects of costs and benefits to these associates need further investigation and should be a focus of future research.

Our findings add to the growing literature with regards to the coexistence and associations of predator and prey species pairs where there is a trade-off between the costs and benefits of the association (Norrdahl *et al.* 1995, Bogliani *et al.* 1999, Thomson *et al.* 2006, Mönkkönen *et al.* 2007). We also provide evidence of costs and benefits for both protected and protective species, the latter of which is often overlooked (Bogliani *et al.* 1999) but is important to gain a full understanding of these interactions.

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## **Conflict of interest**

There are no conflicts of interest in this research.

## **Data availability**

Data are deposited in ZivaHub Digital Repository <https://doi.org/10.25375/uct.24205965>

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