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Research

Cite this article: Little J, Rubenstein DR, Guindre-Parker S. 2022 Plasticity in social behaviour varies with reproductive status in an avian cooperative breeder. *Proc. R. Soc. B* **289**: 20220355.
https://doi.org/10.1098/rspb.2022.0355

Received: 23 February 2022
Accepted: 5 April 2022

Subject Category:
Behaviour

Subject Areas:
behaviour, ecology

Keywords:
behavioural plasticity, individual variation, cooperative guarding, fluctuating environment

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Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.5958603.

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Plasticity in social behaviour varies with reproductive status in an avian cooperative breeder

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Cooperatively breeding vertebrates are common in unpredictable environments where the costs and benefits of providing offspring care fluctuate temporally. To balance these fitness outcomes, individuals of cooperatively breeding species often exhibit behavioural plasticity according to environmental conditions. Although individual variation in cooperative behaviours is well-studied, less is known about variation in plasticity of social behaviour. Here, we examine the fitness benefits, plasticity and repeatability of nest guarding behaviour in cooperatively breeding superb starlings (*Lamprotornis superbus*). After demonstrating that the cumulative nest guarding performed at a nest by all breeders and helpers combined is a significant predictor of reproductive success, we model breeder and helper behavioural reaction norms to test the hypothesis that individuals invest more in guarding in favourable seasons with high rainfall. Variation in nest guarding behaviour across seasons differed for individuals of different reproductive status: breeders showed plastic nest guarding behaviour in response to rainfall, whereas helpers did not. Similarly, we found that individual breeders show repeatability and consistency in their nest guarding behaviour while individual helpers did not. Thus, individuals with the potential to gain direct fitness benefits exhibit greater plasticity and individual-level repeatability in cooperative behaviour.

1. Introduction

Cooperative breeding—when more than two individuals contribute offspring care—occurs most often in birds and mammals living in unpredictable environments [1–4]. In habitats where environmental conditions fluctuate drastically through time, the costs and benefits of offspring care are also likely to vary according to environmental quality [5]. For example, providing offspring care under harsh conditions may be more costly [6], but it may also disproportionately improve the outcome of a breeding attempt (the hard life hypothesis) [7,8]. By contrast, providing offspring care under favourable environmental conditions may be less costly [6], but it may either (i) contribute little to improving breeding success (the hard life hypothesis) [7,8] or (ii) allow additional reproductive benefits given the favourable conditions (the temporal variability hypothesis) [1]. In many cooperatively breeding species, individuals adjust their offspring care effort over time according to current environmental conditions [9–11]. This behavioural plasticity—when one individual alters their behaviour when facing different environmental conditions [12]—is a likely mechanism that would allow individuals of cooperatively breeding societies to track fluctuations in their environments and optimize their contributions to offspring care under fluctuating costs and benefits [13,14]. Unfortunately, surprisingly little is known about plasticity in cooperative behaviours.

A number of socioecological factors contribute to shaping inter-individual variation in cooperative behaviour, including an individual's reproductive status or breeding role [15,16], sex [17], dominance rank or age [18–20], or hormones [21,22], as well as the current size or composition of their social group [23–26], predation risk [27], food availability [28] or weather [11,29]. A growing number of empirical studies have also shown that individuals exhibit consistency in their cooperative behaviour [30]. In banded mongooses (*Mungos mungo*) and meerkats (*Suricata suricatta*), for example, babysitting the young is repeatable [31,32], and in western bluebirds (*Sialia mexicana*) the likelihood of becoming a helper is not only repeatable but also heritable [33]. By contrast, cooperatively breeding cichlids (*Neolamprologus pulcher*) show repeatable cooperative behaviours that are shaped by social interactions but are not heritable [34]. Despite the repeatability of cooperative behaviour in many social species, it remains unclear if and how individuals adjust their behaviour according to fluctuating environmental conditions as few studies have assessed plasticity in cooperation. Indeed, a reaction norm approach—when the behaviour of one individual is measured across a range of environmental conditions—requires large datasets made up of long-term, repeatedly observed behaviours across the same individuals and across different environmental conditions [35]. Understanding whether individuals show plasticity in their cooperative behaviours, as well as whether all individuals show the same type of plasticity in response to environmental fluctuation, will help us to better understand the extent to which organisms living in unpredictable environments may rely on behavioural plasticity to optimize the costs and benefits of cooperation.

Superb starlings (*Lamprotornis superbus)* are plural cooperative breeders that live in large mixed-kin social groups [36] of up to 60 individuals and where multiple breeding pairs will attempt to reproduce every breeding season. The young receive care from both their social parents and from helpers at the nest—between 1 and 15 non-breeding individuals [11,37]. Helpers can be either male or female, related or unrelated to the breeders [37], and contribute to both provisioning the young as well as guarding the nest, though typically perform less offspring care than breeders [11]. Nest predation is very high in this system as over 90% of nest failure is driven by predation [37], making nest guarding (and group defense more generally) an essential cooperative behaviour that has important fitness benefits [11,38]. The costs of providing offspring care are thought to be variable in this species, as rainfall and thus food availability, fluctuate unpredictably from one breeding season to the next [39]. Rainfall influences a number of behaviours in superb starlings; during the pre-breeding period, it shapes the availability of breeding positions within each social group [40], while during the breeding season, it shapes the availability of insects used to provision young and sustain adults during offspring care [11,37]. In addition, the abundance of many superb starling nest predators—including birds of prey and snakes—is also thought to indirectly covary with rainfall as a result of fluctuations in rodent populations [41,42]. Since prior work has shown that nest guarding behaviour is positively correlated to rainfall [11], rainfall is also likely to shape individual contributions to nest guarding behaviour.

Here, we examine whether individual superb starlings show behavioural plasticity by adjusting their nest guarding behaviour across breeding seasons that differ in rainfall using a reaction norm approach. After determining how the cumulative nest guarding effort across all breeders and helpers influences fledging success, we test the hypothesis that seasons of high pre-breeding or breeding rainfall will result in increased nest guarding since individuals will be in better body condition and can choose to devote less time to foraging. This reaction norm approach also allows us to examine whether individuals show the same behavioural plasticity—that is, whether all individuals respond the same way to among-season changes in rainfall—or whether some individuals respond more or less strongly to environmental fluctuations than others. Although behavioural plasticity can also occur within a single breeding season, the focus of our study is on plasticity across breeding seasons where fluctuations in rainfall are more drastic. In addition to exploring behavioural reaction norms for breeders and helpers, we also estimate the repeatability of guarding behaviour across seasons for individuals of each breeding role. Ultimately, this study contributes to our limited knowledge of behavioural plasticity in cooperative species that experience highly fluctuating environmental conditions.

2. Methods

(a) Study system

Since 2001, we have studied a free-living population of superb starlings in central Kenya (Mpala Research Centre; 0°17′ N, 37° 52′ E). Individuals in this population are sexed genetically [43], and individual age is known for birds born in the study population or estimated based on eye colour for immigrants that were born outside the focal social groups we monitor [38]. Birds breed during the rainy seasons, which occur twice a year at our study site: the short rains typically last from October to November, while the long rains last from March to June [44]. Rainfall which is highly variable from year to year in both the pre-breeding and breeding seasons [39,44] is crucial for superb starlings, as it increases the availability of insects, the primary food source for adult birds and the exclusive food source for chicks [39]. We monitored rainfall using an automated Hydrological Services TB3 Tipping Bucket Rain Gauge located at the Mpala Research Centre [45]. Since daily data were not always available from the beginning of the study, we used monthly data to calculate seasonal rainfall for the following periods: the total rainfall for the pre-breeding short rains (July–September), the breeding short rains (October–November), the pre-breeding long rains (December–February) and the breeding long rains (March–June).

(b) Nest guarding observations

We visited nests daily during the rainy breeding seasons, monitoring the number of eggs, nestlings or fledglings for each nesting attempt. When an active nest contained nestlings, we performed focal observations to measure superb starling nest guarding behaviour, where breeders and helpers contribute to guarding the young by spending time within 20 m of the nest [11,37]. Individuals commonly perch on nearby trees or pace the ground: we assume that these behaviours confer an advantage against predators, since superb starlings frequently make alarm calls when they spot predators and mob predators cooperatively [37,46]. While mobbing behaviour is certainly more costly and more directly linked with offspring survival, nest guarding is more frequent and remains a crucial first step to spotting predators that approach the nest and represents a time commitment. All active nests were observed during chick-rearing via focal observations lasting approximately 2 h per observation period [11]. The same nest was observed multiple times when possible, for an average of 5.6 h ± 0.15 at each nest (mean ± s.e.). The identity of each bird arriving within 20 m of the nest was determined with a spotting scope based on their unique combination of coloured leg bands, and guarding was defined as the proportion of time individuals spent present at the nest (but not inside it) relative to the total length of the observation period at that nest. The number of individuals caring for young at a nest was tallied (including parents and helpers). As in prior work, the number of helpers observed increases with the total length of observations performed at a nest [11], so we calculated the residuals of the number of caretakers on observation time and use this as an index of the number of individuals providing care at a nest [11].

(c) Statistical analyses

Our dataset included 1435 guarding bouts across 194 nests, which represented observations of 319 helpers and 148 breeders across nine social groups (mean individuals per group ± s.e. = 111 ± 36.9) [47]. We had repeated observations across multiple breeding seasons for 253 individuals in total, which included 4.33 ± 0.42 repeated measures per individual (mean number of seasons ± s.e.).

To determine if cumulative guarding performed at a nest shaped reproductive success, we used a generalized linear mixed model (GLMM). We built a GLMM using a Poisson distribution where the number of chicks that fledge the nest was our dependent variable. We included total time spent guarding the nest, breeding season rainfall, pre-breeding season rainfall, clutch size and season type (long versus short rains) as fixed effects in the model. We also included a random intercept for social group ID in this model as a random effect.

Next, we identified socioecological predictors of nest guarding by using a preliminary linear mixed model (LMM) to identify the fixed effects we would need to include in subsequent analyses (electronic supplementary material, table S1). We investigated the categorical variables sex and breeding role, as well as the continuous variables clutch size, mean relatedness coefficient (for each social group), the number of adults providing care at that nest (the residuals of number of adults providing care on total observation length) [11], age, breeding season rainfall and pre-breeding season rainfall as fixed effects. We added two interactions to the fixed effects: the interaction between sex and role because mothers often perform more care than others [11], as well as the interaction between relatedness and sex because males are the philopatric sex [37]. Finally, we included bird ID and social group ID as random effects in this model. This approach revealed that sex, breeding role, clutch size and breeding rainfall were the only predictors significantly correlated to nest guarding behaviour. For our subsequent analysis, we modelled breeder and helper nest guarding plasticity separately, and we included sex, clutch size and breeding rainfall as predictor variables to account for their effect on nest guarding behaviour in the reaction norm models.

Finally, to examine individual variation in nest guarding plasticity, we paired an information-theoretic approach and nested LMMs that differed in random slope and intercept structures. This combined approach allowed us to determine whether individuals showed plasticity in guarding behaviour across seasons of differing rainfall, and whether there was among-individual variation in this plasticity in superb starlings based upon whether the random slope model was a better fit to our dataset compared to other models. The first model (the null) included only the fixed effects listed above and a random effect for social group ID. The second model we tested was a random intercept model which added a random intercept for each individual superb starling to the null model. The third model added a random slope for breeding rainfall to the random intercept model, which allowed us to test for individual variation in guarding plasticity as breeding rainfall changed across years. Unfortunately, our dataset was not large enough to allow us to test for a correlation between intercepts and slopes, an approach that requires more statistical power. We compared these three LMMs using Akaike's information criterion (AIC_C) to identify the best-supported model(s), repeating this approach for helpers and for breeders separately. Models with lower AIC_C scores indicate stronger support, and models within two AIC_C values of one another were interpreted to fit a dataset similarly well.

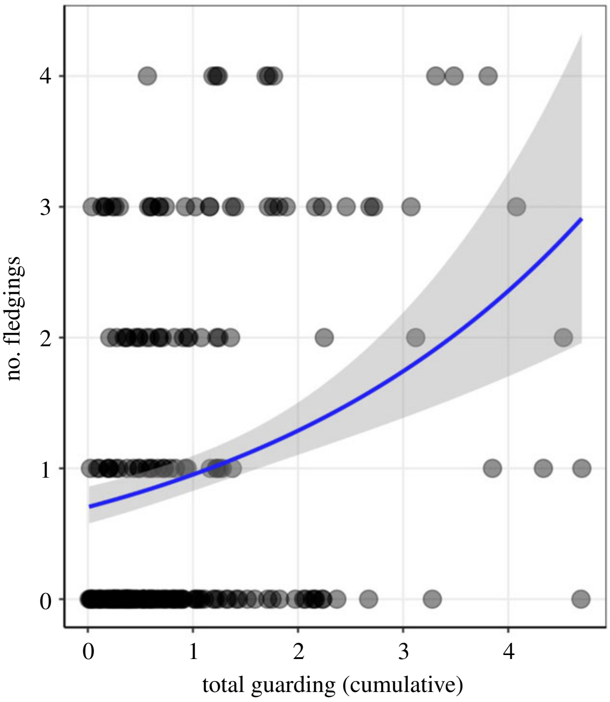

Figure 1. Superb starling nests ($n = 194$) that receive greater cumulative guarding from all breeders and helpers combined are more likely to fledge a greater number of young. The solid line indicates the population-wide relationship between fledglings and cumulative guarding, and the shading shows the 95% CI. (Online version in colour.)

In addition to these models, we estimated the repeatability of nest guarding behaviour for breeders and for helpers separately. Repeatability provides an estimate of individual consistency in nest guarding behaviour across breeding seasons and is calculated as variation among- relative to within-individuals [48]. The statistical significance of a repeatability estimate was determined using a likelihood ratio test (LRT), and parametric bootstrapping was used to calculate 95% confidence intervals (CI; following 1000 bootstraps). We calculated the repeatability of nest guarding behaviour for (i) individual starlings as well as for (ii) each social group using the same model fixed and random effects as defined in Model 2 (with random intercepts for individual ID and for social group ID).

All models were fitted by maximum likelihood, where LMMs and GLMMs were run in R (v. 3.6.1) using the package 'lme4' (v. 1.1-21). Nest guarding was log-transformed, and diagnostic plots revealed that model residuals appeared normally distributed and were not heteroscedastic. We calculated model AIC_C scores and model weights using the 'bbmle' package (v. 1.0.23.1). Finally, we estimated the repeatability of guarding behaviour using the 'rptR' package (v. 0.9.22).

3. Results

(a) Nest guarding and reproductive success

We found that reproductive success—measured as the number of young that fledged a nest—was positively correlated to the cumulative guarding that all starlings performed at a nest (figure 1). However, the number of young fledging the nest was unrelated to clutch size, breeding rainfall, pre-breeding rainfall or season type (long versus short rains), suggesting

Table 1. Results of a GLMM exploring how nest guarding and environmental factors shape the number of fledglings that successfully leave the nest. Asterisks denote significant predictor variables where the 95% CI did not overlap with 0. This dataset included the number of fledglings observed at 194 nests, across nine social groups.

fixed effects	estimate ± s.e.	*z*-value	95% CI
intercept	0.015 ± 0.15	0.10	−0.29 to 0.30
total guarding time	0.29 ± 0.06	4.79	0.17 to 0.41*
clutch size	0.12 ± 0.08	1.52	−0.03 to 0.27
breeding rainfall	0.003 ± 0.11	0.03	−0.20 to 0.21
pre-breeding rainfall	0.11 ± 0.10	1.12	−0.08 to 0.31
season type (short rains)	−0.30 ± 0.25	−1.20	−0.80 to 0.19
random effects	**variance**	**s.d.**	**95% CI (s.d.)**
group ID (intercept)	0.02	0.12	0 to 0.40

that nest guarding behaviour is a stronger predictor of success in superb starlings than rainfall (table 1).

(b) Socioecological predictors of nest guarding behaviour

Our preliminary model identified several factors that shape nest guarding behaviour in superb starlings. Overall, starlings guarded the nest more during seasons of higher breeding rainfall (electronic supplementary material, table S1), which supported our hypothesis that seasons of elevated rainfall—and thus insect availability—allow individuals to spend a greater proportion of their time guarding the nest rather than searching for food. Nest guarding also differed by sex and breeding role, such that females performed more nest guarding than males and breeders guarded more than helpers (electronic supplementary material, figure S1). Guarding was also related to the clutch size at the nest, such that starlings at nests with a larger clutch size guarded more. Surprisingly, we found that guarding behaviour was unrelated to the number of individuals providing care at a nest (as in [11]), or to pre-breeding rainfall. We also found that guarding was not correlated with age, which may be explained by the significant overlap in age between breeders and helpers. The results of this model informed the fixed effects in our subsequent reaction norm models.

(c) Plasticity in nest guarding behaviour

Breeders and helpers differed in their degree of plasticity in nest guarding behaviour (figure 2). Our information-theoretic approach to examine behavioural reaction norms in breeders identified two similar top models that had a combined weight of 99% (table 2): these included model 2 with random intercepts for individual ID, as well as model 3 with random intercepts and slopes that both differ across individuals. The fixed effects of both models are consistent with the previous results that fathers guard the nest less than mothers, and that nest guarding in breeders is positively correlated with clutch size and breeding rainfall (table 3). The random effects of both top models support random intercepts for individual starlings, suggesting that breeders show important individual variation in their nest guarding behaviour. However, in model 3, the CIs for the estimate of the random slopes include 0 (table 3), indicating (i) that a single slope estimated for all breeders fits our dataset similarly well and (ii) that including unique random slopes for each individual breeder does not better explain variance in nest guarding behaviour than a model with random intercepts alone.

For helpers, the results of our information-theoretic approach were equivocal, with two candidate models falling within 2 AICc values of one another (table 1). Model 1 (null model) was the top-ranked model with a weight of 59%, followed by model 2 (intercept only model) with a weight of 25%. Model 3 (random slopes model) has a weight of 16% but was not included in the top set of models (table 2). The fixed effects for the top two models support the conclusion that helpers increase their nest guarding at nests with larger clutches, but guarding behaviour is not correlated with helper sex or breeding rainfall (table 4). The random effect of model 2 did not support that fitting individual intercepts contributed to explaining nest guarding in helpers, as the 95% CIs for this random effect included 0. Taken together, these results do not support individual differences in helper guarding behaviour, nor plasticity in helper nest guarding behaviour across seasons of differing breeding rainfall.

(d) Repeatability in nest guarding behaviour

Repeatability in nest guarding behaviour differed between breeders and helpers. The repeatability of nest guarding behaviour for individual breeders was 0.10 ± 0.05 (mean ± s.e.; 95% CI = 0.01 to 0.21), which was statistically significant according to a LRT (*p*-value = 0.0001). Thus, individual breeders show some consistency in their nest guarding behaviour. By contrast, breeder guarding behaviour was not repeatable at the level of the social group (repeatability = 0.02 ± 0.02; 95% CI = 0 to 0.08; *p*-value = 0.11), suggesting that there are no consistent differences in the group-level guarding behaviour of breeders across different social groups.

In contrast with breeders, the repeatability of nest guarding behaviour for individual helpers was 0.01 ± 0.02 (95% CI = 0 to 0.06), which was not significantly repeatable (*p*-value = 0.28). This suggests that individual helpers do not show consistent differences in their guarding behaviour. Helper guarding behaviour was repeatable across social

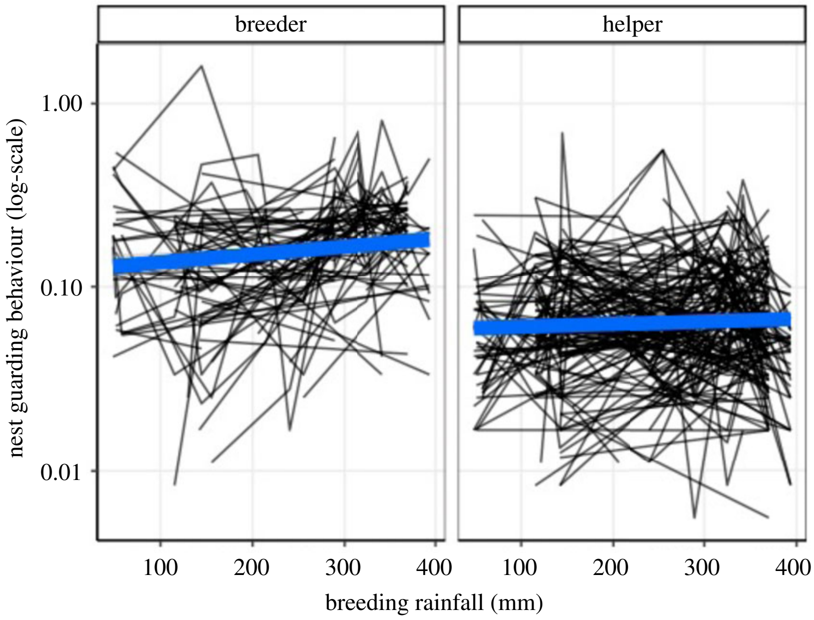

Figure 2. Individual reaction norms of superb starlings, where black lines represent the guarding behaviour of one individual across breeding seasons that differ in their breeding rainfall. The thicker solid line indicates the population-wide relationship between guarding behaviour and breeding rainfall. The *y*-axis is on a natural log-scale. Panels represent data for breeders ($n = 148$) and helpers ($n = 319$). Electronic supplementary material, figure S2 is available to show a subset of reaction norms ($n = 30$) plotted in separate panels for each individual bird. (Online version in colour.)

Table 2. We compared multiple nested models that ranged from no random effect of individual ID (model 1), to including random intercepts for each individual (model 2), and finally to including random intercepts and random slopes allowing for individual starlings to adjust their nest guarding according to breeding rainfall (model 3). We compared the three nested models for each category of breeding role (breeders versus helpers). We identified the best-fitting model(s) using AICc, where all models within 2 ΔAICc of the top model are italicized and can be interpreted to fit the dataset equally well.

breeding role	model	random effects	d.f.	$\mathrm{AIC_C}$	$\Delta\mathrm{AIC_C}$	model weight
breeders	model 1	null	6	1060.5	11.1	0.003
	model 2	*intercept (ID)*	*7*	*1049.4*	*0.0*	*0.72*
	model 3	*intercept (ID), slopes (ID × breeding rainfall)*	*8*	*1051.3*	*1.9*	*0.28*
helpers	*model 1*	*null*	*6*	*2620.0*	*0.0*	*0.59*
	model 2	*intercept (ID)*	*7*	*2621.7*	*1.8*	*0.25*
	model 3	intercept (ID), slopes (ID × breeding rainfall)	8	2622.6	2.6	0.16

groups, however, and social group ID showed a repeatability estimate of 0.02 ± 0.02 (95% CI = 0 to 0.06; *p*-value = 0.001). Thus, while breeders show consistent guarding behaviour at the individual but not at the social group level, helpers show consistent nest guarding behaviour at the social group level but not at the individual level.

4. Discussion

Nest guarding is thought to be a critical cooperative behaviour in superb starlings in light of the high nest predation rates that this species faces [37]. Our study demonstrates that while individuals perform relatively little nest guarding—up to a fifth of their time—the cumulative impact of nest guarding across all individuals that breed or help at a nest is critical to raising young to independence successfully, as it is the single best predictor of fledging success. Despite the potential fitness benefits of increased nest guarding, breeders and helpers differed not only in their mean nest guarding behaviour, but also in the repeatability and plasticity of their nest guarding behaviour across breeding seasons of varying rainfall. Breeders perform more nest guarding than helpers, and nest guarding behaviour in breeders is repeatable, as starling parents showed consistency in their nest guarding behaviour across seasons. In other words, some breeding superb starlings are consistently guarding the nest at higher rates season after season, whereas other breeders are consistently performing less nest guarding each year.

Our results show that guarding behaviour is unrelated to age, suggesting that individual experience is unlikely to explain such differences in behaviour among individuals. In addition to individual consistency in guarding behaviour, breeders also showed plasticity in their nest guarding, such that parents guarded the nest more in seasons of higher breeding rainfall. Our reaction norm approach suggests that all breeders respond to among-season changes in rainfall similarly, however, suggesting that there is no individual variation in behavioural plasticity across breeders (i.e. where one breeder may respond to rainfall more strongly than another).

Table 3. Results of the top LMMs identified in our AIC analysis exploring whether random intercepts and/or random slopes explain variation in nest guarding behaviour across seasons with differing rainfall in breeders. Asterisks denote significant predictor variables where the 95% CI did not overlap with 0. The breeder dataset includes 442 guarding rates across 148 individual starlings.

	model 2 (random intercepts)			model 3 (random intercepts and slopes)		
fixed effects	**estimate ± s.e.**	***t*-value**	**95% CI**	**estimate ± s.e.**	***t*-value**	**95% CI**
intercept	−1.77 ± 0.07	−25.0	−1.93 to −1.63*	−1.78 ± 0.07	−25.1	−1.93 to −1.64*
sex (male)	−0.24 ± 0.09	−2.79	−0.41 to −0.07*	−0.24 ± 0.09	−2.79	−0.41 to −0.07*
clutch size	0.12 ± 0.04	3.15	0.04 to 0.19*	0.12 ± 0.04	3.09	0.04 to 0.19*
breeding rainfall	0.14 ± 0.04	3.77	0.07 to 0.21*	0.14 ± 0.04	3.64	0.06 to 0.22*
random effects	**variance**	**s.d.**	**95% CI**	**variance**	**s.d.**	**95% CI**
social group ID (intercept)	0.01	0.10	0 to 0.26	0.01	0.10	0 to 0.26
ID (intercept)	0.07	0.26	0.15 to 0.38*	0.07	0.26	0.15 to 0.38*
ID × breeding rainfall (slope)	n.a.	n.a.	n.a.	0.01	0.10	0 to 0.27
residual	0.55	0.74	0.69 to 0.80*	0.54	0.73	0.67 to 0.80*

Table 4. Results of the top LMMs identified in our AIC analysis exploring whether random intercepts and/or random slopes explain variation in nest guarding behaviour across seasons with differing rainfall in helpers. Asterisks denote significant predictor variables where the 95% CI did not overlap with 0. The helper dataset includes 1008 guarding rates across 319 individual starlings.

	model 1 (null)			model 2 (random intercepts)		
fixed effects	**estimate ± s.e.**	***t*-value**	**95% CI**	**estimate ± s.e.**	***t*-value**	**95% CI**
intercept	−2.75 ± 0.06	−44.2	−2.89 to −2.63*	−2.76 ± 0.06	−44.1	−2.89 to −2.63*
sex (male)	−0.02 ± 0.06	−0.36	−0.13 to 0.09	−0.02 ± 0.06	−0.35	−0.14 to 0.09
clutch size	0.07 ± 0.03	2.37	0.01 to 0.12*	0.07 ± 0.03	2.40	0.01 to 0.12*
breeding rainfall	0.05 ± 0.03	1.72	−0.01 to 0.10	0.05 ± 0.03	1.77	−0.01 to 0.10
random effects	**variance**	**s.d.**	**95% CI**	**variance**	**s.d.**	**95% CI**
social group ID (intercept)	0.02	0.12	0.06 to 0.25*	0.02	0.12	0.05 to 0.25*
ID (intercept)	n.a.	n.a.	n.a.	0.01	0.10	0 to 0.23
ID × breeding rainfall (slope)	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
residual	0.77	0.88	0.84 to 0.92*	0.76	0.87	0.83 to 0.92*

By contrast, superb starling helpers showed no repeatability or plasticity in their nest guarding behaviour—we only found evidence for repeatability in helper guarding behaviour at the social group-level, suggesting that helpers in some social groups consistently guard the nest more relative to other social groups. For both individual-level breeder guarding and group-level helper guarding, we found significant but low repeatability estimates (0.1 and 0.02, respectively)—these estimates are lower than those previously reported for cooperative care behaviours in meerkats, banded mongooses and western bluebirds which ranged between 0.1 and 0.5 [31–33] as well as the mean repeatability of behaviour (0.37) as reported in a meta-analysis of over 750 studies [49]. Repeatability in superb starling nest guarding behaviour is thus much lower than other behavioural traits, perhaps because numerous extrinsic factors—including rainfall—can shape nest guarding decisions in this species.

One explanation for why breeders show plasticity in nest guarding, while helpers do not, may be that the relative costs and benefits of guarding differ with reproductive status (i.e. different breeding roles). Only individuals that have the potential to gain direct fitness gains exhibit plasticity and repeatability in their care behaviours, whereas helpers that would gain indirect benefits only do not. Like breeders, individual helpers clearly can and do adjust their guarding behaviour across different breeding seasons; they just do not appear to use rainfall as a cue for their investment in guarding behaviour. While prior work in superb starlings found no evidence that guarding the nest resulted in short-term physiological costs of caring for young [22], breeders do perform more offspring care on average than helpers [11] and may therefore benefit most from adjusting nest guarding according to the current rainfall that they face. In support of this idea, mother superb starlings are most likely to use a load-lightening strategy to reduce their offspring care effort in the presence of more helpers [11]. For helpers, however, there may be limited value in adjusting nest guarding behaviour according to current rainfall if nest guarding is not particularly costly to perform or only performed opportunistically. We originally hypothesized that one of the costs of performing guarding included loss of foraging opportunity, since periods of lower rainfall result in lower maternal body condition [37]. Individuals that provision the young most, however, also tend to spend more time guarding the nest (spearman rank correlation test S; $\rho = 0.69$, p-value $<$ 0.001), which suggests that superb starlings do not show task specialization (similarly to other cooperative breeders [50]) and that more committed breeders and helpers perform more offspring care in general. These patterns support the idea that individuals that guard the nest a greater proportion of the time are still able to find enough food to provision the young. An alternative possibility is that some predators, many of which eat starling eggs or nestlings, are more common in periods of high rainfall [41,42]—this increased predation risk could drive plasticity in guarding in breeders (who have already invested more in each breeding attempt) but not in helpers.

While rainfall may shape a number of important decisions in subordinate superb starlings including the adoption of different breeding roles [37], whether to breed for the first time [40], and whether to disperse from the natal group [37], it appears that seasonal differences in rainfall may actually have a limited influence on nest guarding decisions for helpers. One possibility is that a helper's quality (e.g. physiological state or body condition) may play a more important role in shaping nest guarding decisions. Body condition has been shown to shape or limit offspring care in cooperatively breeding species, including in pied babblers (*Turdoides bicolor*) [51] and meerkats (*Suricata suricatta*) [52]. Similarly, superb starling glucocorticoid levels prior to offspring care shape subsequent investment in nest guarding behaviour [22]. An alternative would be for variation in individual quality to explain the repeatable differences in guarding behaviour observed by breeders. Unfortunately, we lack data to test how superb starling body condition or hormone levels shape nest guarding behaviour and/or plasticity in this behaviour. Another explanation as to why superb starling helpers may not adjust their nest guarding behaviour according to fluctuations in rainfall is that the time scale over which rainfall was measured is too long relative to the time scale over which behavioural decisions are made. For example, day-to-day changes in the social or abiotic environments of individuals may play a larger role in shaping offspring care [53] compared to longer-term seasonal fluctuations as measured in this study. Indeed, while rainfall plays an important role in shaping a variety of critical decisions in superb starlings (e.g. breeding role, first breeding attempt and timing of dispersal), these represent major transitions rather than fine-scale behaviours. Environmental conditions on short time scales—such as daily weather—have been shown to shape offspring care behaviours in several species including tree swallows (*Tachycineta bicolor*) [54], blue tits (*Cyanistes caeruleus*) [55], North American red squirrels (*Tamiasciurus hudsonicus*) [56] and arctic ground squirrels (*Urocitellus parryii*) [56]. It is possible that breeders responded to rainfall on a longer time frame and helpers only responded to rainfall on a short time frame, which was not captured in our study. Finally, although age and mean relatedness were not predictors of nest guarding, it remains possible that differences in dispersal, survival or relatedness—where breeders are more likely to persist in the social group and be related to the young—could explain the differences that we observed in nest guarding behaviour across breeding roles.

In conclusion, we found that the cumulative guarding at a nest increased the number of young that fledged and was more influential than the original clutch size or environmental conditions during the breeding season on reproductive success. This is perhaps not surprising, since nest predation is the leading cause of reproductive failure in superb starlings [11,37] and predation risk may shape the evolution of sociality [57]. While breeders but not helpers adjust their nest guarding behaviour in response to fluctuations in rainfall, cumulative nest guarding increases most when a greater number of helpers participate in providing care at a nest [11]. Protection against predators may be among the most important selective factors that favour sociality and cooperative offspring care in superb starlings, since prior work showed that adult survival increases with social group size [38], and now this study suggests fledging success increases with cooperative nest guarding. Despite these important fitness consequences, nest guarding behaviour repeatability and plasticity differ for breeders and helpers, possibly due to the difference in potential direct versus indirect fitness benefits gained from performing a cooperative act. Ultimately, this study contributes to our limited knowledge on behavioural plasticity in cooperative species by showing that breeders, who stand to gain direct fitness from caring for young show greater repeatability and plasticity of offspring care than do helpers. Future work on the causes of variation in repeatability or plasticity in cooperativeness will be necessary to better understand the costs and benefits of cooperation and ultimately the evolution of cooperative breeding behaviour.

Ethics. This study uses a long-term dataset. The original fieldwork was conducted as approved by Kenya's National Commission for Science, Technology and Innovation, Kenya's National Environmental Management Authority, the Kenya Wildlife Service and the Mpala Research Centre. All free-living animals were studied as approved by Columbia University's IACUC.

Data accessibility. Data and code are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.02v6wwq3j [47].

Authors' contributions. J.L.: conceptualization, formal analysis and writing—original draft; D.R.R.: conceptualization, data curation, funding acquisition, supervision and writing—review and editing; S.G.-P.: conceptualization, formal analysis, funding acquisition, supervision and writing—original draft.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. We also thank our sources of funding: S.G.-P. was supported by the US National Science Foundation (grant no. IOS-1501257), the Natural Science and Engineering Research Council of Canada, Columbia University and Kennesaw State University. D.R.R. was supported by the US National Science Foundation (grant nos IOS-1121435, IOS-1257530 and IOS-1439985).

Acknowledgements. We are grateful to W. Watetu, G. Manyaas and J. Mosiany for their assistance in the field, as well as S. Caro, S. Shah and field assistants who have helped to collect and organize data since 2001. We thank two anonymous reviewers whose feedback improved this manuscript.

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