

ENVIRONMENTAL STUDIES

Altruistic bet-hedging and the evolution of cooperation in a Kalahari bird

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Altruism is globally associated with unpredictable environments, but we do not understand why. New theory has highlighted that unpredictable environments could favor the evolution of altruism if altruistic acts reduce environmentally induced variance in the reproductive success of relatives (“altruistic bet-hedging”). Here, we show that altruism does indeed reduce environmentally induced reproductive variance in a wild cooperative bird. Our decade-long field study reveals that altruistic helping actually has no overall effect on the mean reproductive success of relatives but instead reduces their reproductive variance. This remarkable pattern arises because helpers improve reproductive performance in dry conditions but reduce it in wet conditions. Helpers thereby specifically reduce rainfall-induced reproductive variance, the very mechanism required for altruistic bet-hedging to explain the enigmatic global association between avian altruism and unpredictable rainfall.

INTRODUCTION

Explanations for the evolution of altruism via kin selection typically focus on scenarios in which altruistic acts yield indirect fitness benefits to the actor by increasing the mean reproductive success of relatives (1). However, recent theory has highlighted that kin selection can also favor altruistic acts if they decrease variance in the reproductive success of relatives in unpredictable environments, a scenario termed “altruistic bet-hedging” (2). Altruistic bet-hedging thus integrates the rationale of kin selection (1) with the long-recognized potential for selection to favor bet-hedging strategies, which decrease the variance in reproductive success arising from unpredictable fluctuations between harsh and benign conditions (3). Selection is expected to favor these reductions in reproductive variance because additional offspring contribute disproportionately to relative fitness under harsh conditions, when competitors are producing few (2, 3). Global associations between altruistic helping behavior (helping to rear the offspring of others) and unpredictable environments (4, 5) highlight a potentially widespread role for altruistic bet-hedging in the evolution of cooperation (6). However, compelling evidence that altruistic helping does indeed reduce environmentally induced variance in the reproductive success of relatives remains elusive (6–11).

White-browed sparrow-weavers (*Plocepasser mahali*) are cooperatively breeding birds that live in extended family groups, occupying year-round territories throughout the semi-arid regions of East and Southern Africa (12–14). Within each social group, a single dominant female (hereafter the “mother”) and male completely monopolize within-group reproduction and 0 to 10 nonbreeding subordinates (hereafter “helpers”) of both sexes help feed the dominants’ nestlings (Fig. 1, A and B) (12, 15). Helping behavior has the potential to yield indirect fitness benefits, as helpers are typically offspring of the dominant pair (12, 16), leaving them closely related to both the dominants and the offspring that they help to rear ($r_{\text{helper-dominants}}$ mean \pm SE = 0.362 ± 0.011 ; $r_{\text{helper-offspring}}$ = 0.341 ± 0.010 ; Supplementary Text A). As their semi-arid environment is characterized

by a highly variable rainfall regime (see Supplementary Text B for temporal and spatial variation in rainfall at our Kalahari study site), helping behavior in this species could well yield indirect fitness benefits via reductions in the environmentally induced variance in reproductive success of related breeders, as envisaged under altruistic bet-hedging (2).

RESULTS AND DISCUSSION

While helpers of both sexes feed nestlings, female helpers do so at substantially higher rates than males (Fig. 1C), and only female helpers have a causal positive effect on the overall rate at which broods of nestlings are fed (hereafter, the “total provisioning rate”). Within-mother variation in female helper number, among her different monitored breeding attempts, strongly positively predicts total provisioning rate (Fig. 1D and table S1; see also Supplementary Text C), while within-mother variation in male helper number does not (Fig. 1E and table S1). Accordingly, the experimental removal of female helpers significantly reduced total provisioning rate, while the experimental removal of male helpers did not (Fig. 1F; Supplementary Text C).

To investigate the effects of this helping behavior on both the mean and variance in reproductive success of mothers, we conducted Bayesian bivariate statistical modeling using our decade-long life history dataset (400 broods born to 68 mothers across 36 social groups). This approach allows the effect of helpers on variance in reproductive success to be assessed directly by comparing the variance components of reproductive success between two categories of mothers with contrasting numbers of helpers (e.g., for mothers with no versus some female helpers; see Materials and Methods for full rationale). As sparrow-weaver helpers only contribute to posthatching offspring care (they do not feed the mother or incubate), our bivariate models investigated the effects of helpers on the number of nestlings that fledged from a given breeding attempt (hereafter “reproductive success”) while controlling for variation in the initial number of hatchlings (see Materials and Methods).

Our analyses reveal that mothers with female helpers do not have a higher mean reproductive success than those without [estimate (95% credible interval) for the difference in mean reproductive success (i.e., model intercept) between the two classes of

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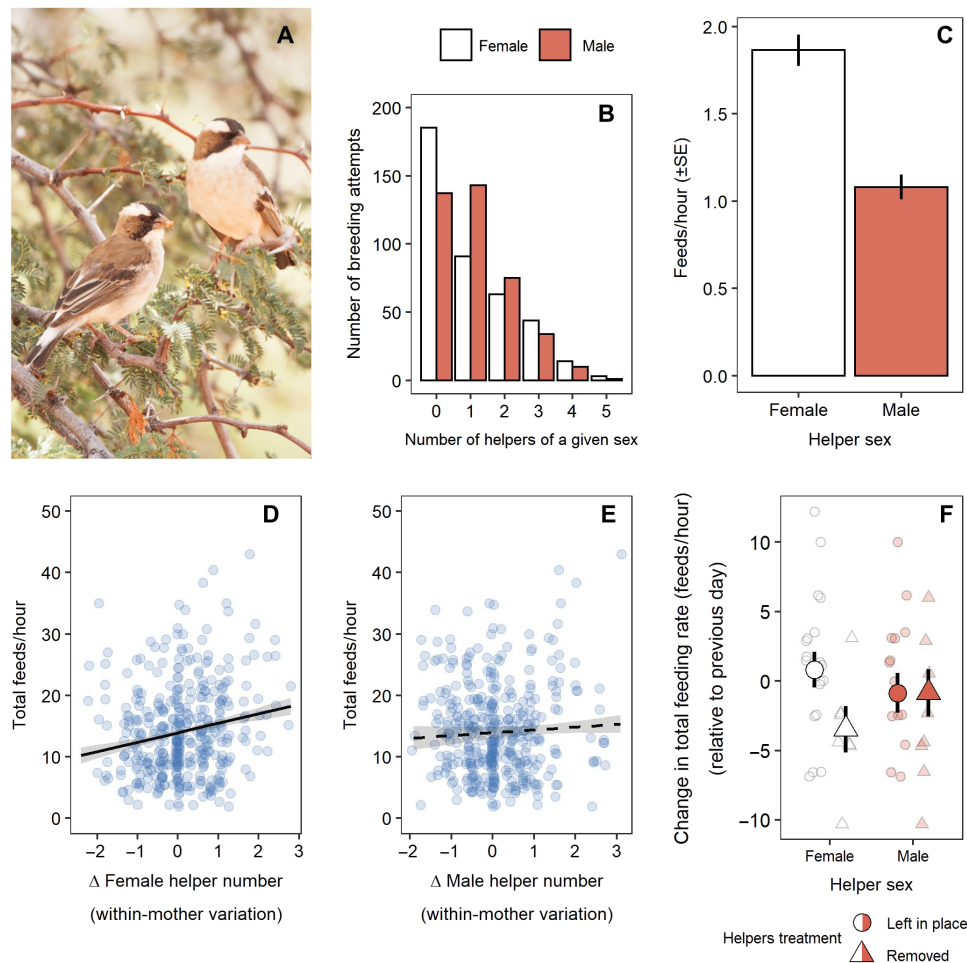


Fig. 1. Helping behavior and its impact on offspring provisioning. (A) A female helper (foreground) carrying a food item for the nestlings of the breeding female (background). (B) Frequency of female and male helper numbers across 400 broods born to 68 mothers across 36 social groups. (C) Female helpers feed nestlings at a significantly higher rate than male helpers [linear model of log-transformed provisioning rate: estimate for “male” effect (\pm SE) = $-0.16 (\pm 0.02)$; Δ AIC (Akaike’s information criterion) on removal of helper sex predictor = 30.62; $n = 1154$ provisioning days recorded for 270 helpers feeding 128 broods across 34 groups]. (D) Within-mother variation in female helper number (Δ female helper number) positively predicts total provisioning rate (Δ AIC = 5.80; table S1), while (E) within-mother variation in male helper number (Δ male helper number) does not (table S1). (F) Experimental removal of female helpers reduced total provisioning rate (relative to the previous day) significantly more than a non-removal treatment (Δ AIC = 4.17), while the experimental removal of male helpers did not (Supplementary Text C). Dots show raw data. Mean model predictions (\pm SE) are shown in (C) to (F). Photo credit: Andrew Young, University of Exeter.

mother = $-0.09 (-0.41, 0.22)$; table S2] but instead show markedly lower variance in reproductive success (Fig. 2A and table S2). These patterns cannot be attributed to confounding effects of variation among mothers or their territories, as within-mother variation in female helper number also predicted the mother’s variance in reproductive success (Fig. 2B and table S2) and not her mean reproductive success [estimate (95% credible interval; CI) for the intercept difference = $-0.16 (-0.44, 0.12)$; table S2]. Nor can these patterns be attributed to variation in maternal age, as maternal age is not correlated with female helper number [maternal age does not outperform a null (intercept only) model in predicting female helper number: Δ AIC (Akaike’s information criterion) = $+0.3$; $n = 124$ breeding attempts by 25 mothers of known (± 15 days) age]. Our inability to detect an effect of female helpers on mean maternal reproductive success cannot be attributed to (i) the need to categorize helper numbers when using this bivariate approach (as univariate modeling confirms that continuous variation in female helper

number does not predict mean maternal reproductive success either; Fig. 2, C and D) or (ii) correlated variation in maternal egg investment concealing a helper effect on mean reproductive success (17) (as no such helper effect is revealed when variation in egg volume or hatchling mass is also statistically controlled; table S3). Conducting similar analyses for male helper numbers revealed no detectable effects of male helpers on the mother’s mean or variance in reproductive success (table S4).

Our finding that variance in maternal reproductive success is reduced specifically in the presence of additional female helpers but not male helpers is important, as it implicates altruistic helping behavior as the likely cause of this variance mitigation rather than correlated effects of group size. The variance reduction could conceivably have arisen because mothers with additional helpers simply live in larger groups, which might yield benefits such as reduced predation risk while foraging, independent of any helping behavior (18, 19). If this was the case, then one would expect additional male

and female helpers to have comparable effects on maternal reproductive variance, as all members of sparrow-weaver groups live and forage together and male and female helpers contribute similarly to both cooperative vigilance and territorial defense (12, 20, 21). However, our findings indicate that maternal reproductive variance is reduced specifically in the presence of additional female helpers, which implicates helping behavior per se as the likely cause, as female helpers help at substantially higher rates than males (Fig. 1C) and only female helpers have causal additive effects on total provisioning rate (Fig. 1, D and F).

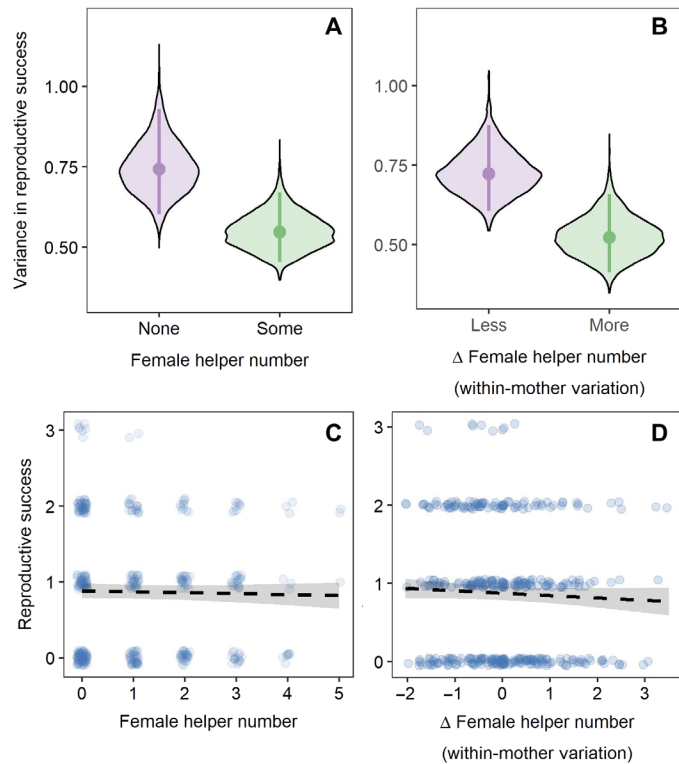


Fig. 2. The effects of female helpers on the mean and variance in reproductive success of related breeders. (A) Bivariate modeling yielded strong evidence that mothers with some female helpers experience lower variance in reproductive success than mothers with no female helpers. (B) This result holds when we isolate the effect of within-mother variation in female helper number. (A) and (B) show estimates of the residual variance in reproductive success for mothers assisted by (A) “None” or “Some” female helpers and (B) “Less” or “More” female helpers than each mother’s own mean female helper number (table S2). We found a significant difference between the residual variance estimates for the two helper number classes [difference estimate (95% CI): (A) None – Some = 0.197 (0.002, 0.392); (B) Less – More = 0.205 (0.025, 0.386)]. Reproductive success was characterized as the number of nestlings that fledged [which predicts the number of fledglings that survived to 1 year; Pearson’s correlation coefficient (r) (95% confidence interval) = 0.77 (0.73, 0.81)] in an analysis that controlled for variation arising from the number of nestlings that hatched (table S2). Shaded areas reflect posterior distributions from two MCMC runs, and the points and error bars reflect the median values and 95% CI for the residual variance estimates (table S2). Univariate modeling confirmed that continuous variation in female helper number does not predict mean reproductive success either (C) before or (D) after isolating the effects of within-mother variation in female helper number [the top models did not contain female helper number (C) or Δ female helper number (D) as a predictor; table S3]. Raw data (transparent blue dots) and mean model predictions (\pm SE) are shown.

The above findings suggest that altruistic helping behavior in sparrow-weaver societies reduces variance in the reproductive success of related breeders. However, altruistic bet-hedging refers to a scenario in which altruism reduces reproductive variance arising specifically from unpredictable environmental variation (2), and global comparative studies of the evolution of cooperation in birds hypothesize that the relevant environmental variable is rainfall (4, 22). The rainfall conditions for our Kalahari study population satisfy the key conditions required for altruistic bet-hedging, by being both highly unpredictable over time and synchronous over spatial scales that far exceed the dispersal distance of our study organism (fig. S1; Supplementary Text B) (2, 3). To investigate whether helping does specifically mitigate rainfall-induced variance in reproductive success, we then tested for the required statistical interaction between female helper number and rainfall in a univariate model of nestling survival to fledging (see Materials and Methods). As rainfall could affect reproductive success over a range of time scales in this arid-zone species, we first used a sliding window optimization approach (Supplementary Text D) (23) to establish that nestling survival was most strongly predicted by the total rainfall that fell between 36 days before hatching and 9 days after hatching (fig. S2). Our modeling then confirmed that the statistical interaction between the total rainfall during this window and female helper number strongly predicts nestling survival, as expected under altruistic bet-hedging (Fig. 3A and table S5). The number of female helpers positively predicts nestling survival in dry conditions but negatively predicts nestling survival in wet conditions (we return to this negative relationship below), an interaction that leaves mothers with markedly lower rainfall-related variation in nestling survival when they have more

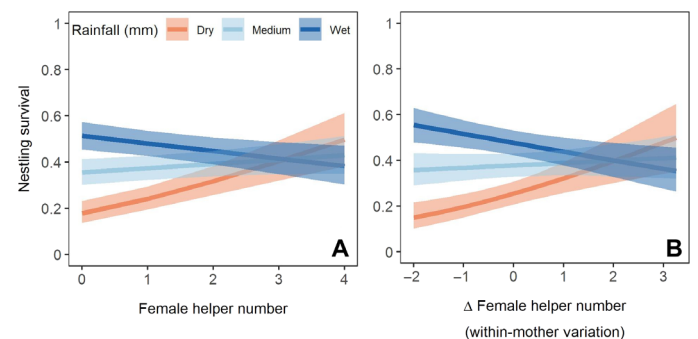


Fig. 3. Helpers mitigate rainfall-induced variation in reproductive success. (A) While rainfall-induced variation in nestling survival to fledging is high in the absence of female helpers (zero on the x axis), mothers with more female helpers experience lower rainfall-related variation in nestling survival because nestling survival is strongly predicted by an interaction between rainfall and female helper number. This interaction was apparent both (A) when modeling the effects of population-level variation in female helper number (see table S5) and (B) when isolating the effect of within-mother variation in female helper number (Δ Female helper number; see table S6). Rainfall and female helper number were not correlated [Pearson’s correlation, r (95% confidence interval) = 0.006 (–0.093, 0.104)]. Plots present mean (\pm SE) model predictions for broods that experienced either (i) no rainfall during the focal rainfall window (Dry, orange), (ii) a medium level of rainfall (Medium, light blue; the prediction for total rainfall = 55.5 mm, the lower tertile of the nonzero total rainfall distribution for the focal rainfall window), or (iii) a high level of rainfall (Wet, dark blue; the prediction for total rainfall = 94.4 mm, the upper tertile of the nonzero total rainfall distribution). n = 341 broods; 132 broods experienced <55.5 mm of rainfall; 99 broods experienced 55.5 to 94.4 mm of rainfall; and 110 broods experienced >94.4 mm of rainfall.

female helpers (Fig. 3A). Again, this pattern holds when we isolate the effects of within-mother variation in female helper number (Fig. 3B and table S6). Male helper numbers, by contrast, did not predict nestling survival, either in isolation or via interactions with rainfall (table S5).

This striking interaction suggests that the apparent negative effect of female helpers on variance in maternal reproductive success revealed by our bivariate analyses (Fig. 2, A and B) does arise, in part, from helpers reducing rainfall-induced variance in reproductive success, as envisaged by global comparative studies of the evolution of cooperation in birds (4, 5, 22). To demonstrate that this is the case, we then integrated rainfall (in the focal window) into our original bivariate models as an additional fixed effect predictor. This confirmed that rainfall has a stronger effect on reproductive success in groups with fewer female helpers than in groups with more female helpers (table S7; as expected given Fig. 3, A and B). Allowing for this effect then renders the difference in residual variance in reproductive success between mothers with fewer and more female helpers no longer significant (table S7), just as one would predict if helpers were principally reducing rainfall-related variance in reproductive success.

The lack of an overall effect of helpers on the mean reproductive success of related breeders arises because positive effects of helping in “dry” conditions (i) are no longer apparent under “medium” levels of rainfall (likely because rain-related increases in food availability reduce maternal reliance on helpers) and (ii) are countered, when integrating across environmental conditions, by a negative effect of helpers in “wet” conditions (Fig. 3). We suspect that this negative effect of helpers in wet conditions may reflect a change in the primary cause of nestling mortality from starvation under dry conditions (which should be mitigated by the causal positive effects of female helpers on total provisioning rate; Fig. 1) to nest predation under wetter conditions [which could conceivably be exacerbated by the positive effect of female helpers on nest visit rate, if provisioning visits leave nests more conspicuous to predators (24)]. While nest predators [such as birds, mongooses, and snakes (25)] may rarely leave signs of their actions, analyses with restricted datasets that attend to the circumstances of nestling mortality are at least consistent with this view: Under higher rainfall conditions, when sparrow-weavers provision their nestlings at higher rates (Supplementary Text E), the absolute risk of nestling starvation appears to decrease while the absolute risk of whole-brood predation is unaffected (fig. S3, A and B). As a consequence, the proportional contribution that predation makes to nestling mortality is greater under higher rainfall conditions (fig. S3C). Therefore, any effect of helpers on nest predation risk would contribute disproportionately to the overall helper effect on nestling survival in wetter conditions. Whether the positive effect of female helpers on nest visit rate does indeed increase nest predation risk (24), however, is not yet known.

One might expect the negative effect of helping under wet conditions to have favored a plastic helping strategy, rather than a bet-hedging strategy (2, 3), in which helpers actually refrained from helping under wet conditions. However, our analyses suggest that the time window during which fallen rain can still influence whether helping has a positive or negative effect stretches a full 9 days into the nestling period (see above), leaving it impossible for helpers to determine the likely impact of their contributions until helping is well under way (as rainfall is unpredictable; Supplementary Text B).

Where unpredictable environments preclude the evolution of adaptive plasticity, selection is instead expected to favor bet-hedging strategies that reduce the variance in reproductive success arising from unpredictable fluctuations between harsh and benign conditions (2, 3, 26). Selection is generally envisaged to favor these strategies because each additional offspring contributes more to relative fitness under harsh conditions, when competitors are producing few (2, 3) [i.e., helping’s positive effect on offspring production in dry conditions will outweigh its negative effect in wet conditions when expressed in relative fitness terms (2)]. Ecological processes have the potential to compound these effects too, further strengthening selection for bet-hedging strategies. For example, offspring production under harsh conditions could have even stronger effects on relative fitness if harsh conditions also reduce adult survival.

Under altruistic bet-hedging, helping is favored by selection because it reduces the environmentally induced reproductive variance of relatives (2). While this scenario does not preclude helping also yielding some benefit via alternative mechanisms (2), the absence here of a detectable net positive effect of helping on the mean reproductive success of relatives is notable, as it highlights the likely importance of the evident effect of helping on reproductive variance. While the above analyses focus on helper effects on offspring survival, sparrow-weaver helpers also have no detectable effect on the mean clutch sizes or re clutching rates of mothers (alternative routes through which helping could yield indirect fitness benefits) (27). Helping could, however, yield additional indirect fitness returns via other mechanisms [e.g., by improving breeder survival and/or offspring quality (rather than offspring survival)] and could also conceivably yield direct fitness benefits. The most credible mechanism through which helping could yield direct fitness benefits to helpers across the social vertebrates is if it increases group size by improving offspring survival or breeder reproductive rate, as helpers may stand to benefit from living in a larger group [the group augmentation hypothesis (18)]. It is notable then that helping in sparrow-weaver societies does not improve offspring survival on average (Fig. 3) or breeder reproductive rate (27) and so will not tend to augment group size.

Together, our findings strongly suggest that helping behavior in sparrow-weaver societies reduces the environmentally induced variance in reproductive success of related breeders, as envisaged for an altruistic bet-hedging strategy (2). Moreover, helping appears to specifically mitigate rainfall-related variance in reproductive success, the very mechanism required for altruistic bet-hedging to explain the hitherto enigmatic global association between avian altruism and unpredictable rainfall regimes (4, 5, 22). A more widespread role for environment-dependent helper effects of this kind could explain not only why avian altruism is associated with variable environments (4, 5, 22) but also why altruism can be associated with dry environments too (28, 29); helping can reduce reproductive variance in variable environments while having its strongest positive effects on mean reproductive success in environments that are consistently dry (Fig. 3). As few studies to date have sought to dissect the effects of altruism on both the mean and variance in performance of relatives (6, 9), the extent to which our findings do generalize to other cooperative organisms is not yet clear. Notably though, helping might generally be expected to have a more beneficial effect on reproductive outcomes under harsher conditions, when rearing offspring unaided may be challenging [dry versus medium in Fig. 3 (8, 30)]. Hence, the resulting beneficial effect of helping on

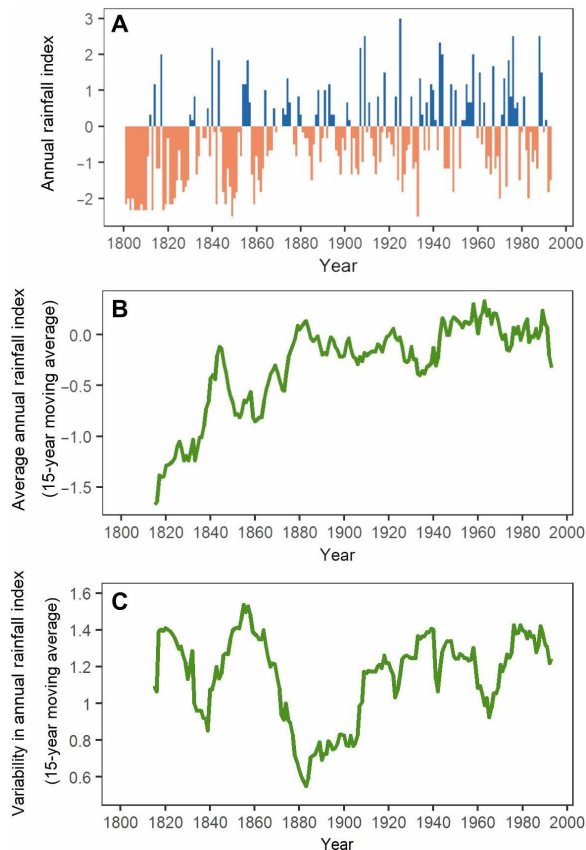


Fig. 4. The implications of Kalahari rainfall patterns over the last two centuries. (A) Annual rainfall index. Positive values (blue) denote wetter years than the recent average, whereas negative values (orange) denote drier years. (B) Average annual rainfall index in moving windows of 15 years. (C) Variability of the annual rainfall index (SD of the annual rainfall index calculated for moving windows of 15 years). As the effects of helping in Kalahari sparrow-weaver societies are rainfall dependent (Fig. 3), these long-term temporal fluctuations in both the mean and variability of rainfall highlight that the extent to which historical selection for helping arose from effects on the mean versus the variance in reproductive success of relatives is itself likely to have fluctuated over evolutionary time. For example, the panels reveal the region's prolonged drought at the start of the 19th century [thought to have started around 1790 (42)], during which the positive effect of helpers on reproductive success under dry conditions (Fig. 3) could have dominated, leading to a transient net positive effect of helping on mean reproductive success during that time. These analyses use a historical rainfall time series from (42), provided by the study's authors.

the environmentally induced reproductive variance of breeders (because the dry and medium lines converge; Fig. 3) could itself prove more widespread as more such studies accrue.

Our findings also highlight a fundamental challenge for attempts to draw inference about historical patterns of selection on cooperative behavior (4, 5, 22). Whenever helping is found to reduce the environmentally induced reproductive variance of relatives (as here), the extent to which kin selection for helping arises via helper effects on the mean versus the variance in reproductive success of relatives will itself be sensitive to longer-term changes in the prevailing environmental conditions. This is because helping can only compress environmentally induced reproductive variance if it has different effects on reproductive success in different conditions (e.g., the different rainfall conditions in Fig. 3). Wherever this is the case, changes

in the relative frequencies of these conditions over time or space can be expected to affect the overall effect of helpers on both the mean and variance in reproductive success of relatives (Fig. 4). Given the potential for marked changes in climatic conditions over evolutionary time, the evolutionary history of altruism in any given clade could conceivably have been characterized by fluctuations in the relative importance of classical net positive effects of helping on the mean reproductive success of relatives (1) and the variance reduction effects more recently envisaged under altruistic bet-hedging (2).

MATERIALS AND METHODS

Study species, population, and general field monitoring

Our study population of ~40 social groups occupies ~1.5 km² of Kalahari thornveld in Tswalu Kalahari Reserve in the Northern Cape Province of South Africa (27°16'S, 22°25'E). Data were collected continuously from September/October to April/May, the Southern summer (hereafter the "breeding season"), between 2007 and 2016 inclusive (nine consecutive breeding seasons). Groups were easily monitored and distinguished in the field as all group members foraged, weaved and defended their territory together, and roosted in individual woven chambers in a single tree or cluster of trees close to the center of their territory (12). Each group contained a single dominant female and male (the breeding pair) and 0 to 10 non-breeding subordinate birds (Fig. 1B) (12). The dominant female lays all of the eggs, and the dominant male completely monopolizes within-group reproduction; twelve to 18% of offspring are sired by extra-group males (typically dominant males in other groups) (12). Dominant pairs were easily identified in the field, as they regularly engaged in conspicuous vocal duets, foraged in close association, and were behaviorally dominant to other group members (12, 31). Male birds could be readily distinguished from females, after 6 months of age, because of their darker bills (12). All birds were fitted with a single metal ring and three color rings for identification (under SAFRING license 1444).

Throughout the breeding season, groups were monitored every 1 to 2 days to determine the date of clutch initiation (when the first egg was laid) and completion [when the last egg was laid; modal clutch size was 2 (range, 1 to 4)]. Clutches were then checked again 8 days later (to confirm the successful progression of incubation), and daily checks then resumed after another 7 days to determine the fate of every egg (hatched or failed). The date on which the first nestling hatched was considered day 1 of the breeding attempt. Broods were then visited every 4 days to monitor nestling survival (i.e., days 1, 5, 9, 13, and 17 of the breeding attempt), and the nestlings were ringed on day 13. Nest checks were discontinued on day 17 to avoid triggering premature fledging. From day 20, field observations and targeted catching sessions were prioritized to determine fledging success, and regular checks of any new nests were resumed to ensure the detection of new clutches.

Group compositions were assessed throughout the breeding season via field observations using spotting scopes (identifying birds via their colored leg ring combination) approximately once a week. The number of male and female helpers (i.e., subordinate group members) present for a given brood was calculated as the daily average number present between days 1 and 24 of the breeding attempt (i.e., the entire nestling period; helper numbers typically remain constant throughout this time). As young offspring contributed little to the provisioning of subsequent broods reared in the

same breeding season, individuals were not considered helpers until they reached the breeding season following that of their birth. Ethical approval for all protocols was provided by the University of Pretoria Animal Ethics Committee (EC023-07, EC100-12, and EC007-17).

Provisioning behavior

Nestling provisioning behavior was recorded using video cameras between days 8 and 13 of the nestling period, for 159 broods being reared by 35 social groups. At least 5 days before video data collection started, we caught every bird in the group (by flushing them from their individual roost chambers at night into a customized capture bag) apart from the dominant female (easily avoided as she roosts in the breeding nest) to confirm group composition and mark each bird's vent feathers with a unique black dye mark to facilitate their identification on provisioning videos (15). On recording days, video cameras were set up in the morning at a standardized time following sunrise to record the provisioning birds flying into and out of the enclosed nest, for approximately 3 hours per day [yielding a total of 392 days of recording over the 159 monitored broods; median of 3 (range, 1 to 5) days per brood]. Additional within-nest cameras have previously confirmed that all nest visits during this time, in which the birds are not conspicuously carrying grass (events that were readily excluded from our provisioning rate calculations), entail the visiting bird carrying a single food item to the nest and delivering it to the chicks (32). The videos were subsequently transcribed to determine the timing of each provisioning visit and the identity of the provisioning bird [using its unique vent mark and information from its leg rings and bill coloration (which reveals its sex; see above)]. This yielded a dataset of the rates at which individual birds provisioned the brood (e.g., Fig. 1C) and the total provisioning rate of the entire group [e.g., Fig. 1 (D and E) and table S1].

Helper removal experiment

To investigate the causal link between the number of helpers in a group and the total provisioning rate that the offspring received, we carried out a helper removal experiment in February and March 2017. Successive broods (and the social groups feeding them) were alternately allocated to either a "removal" or "control" treatment once their first-hatched chick had reached 10 days old. Groups that did not contain helpers (i.e., unassisted breeding pairs) were excluded from both treatments. Provisioning behavior for each brood was monitored following the standard protocol (see above). In removal treatment groups, we caught every subordinate individual from their sleeping chambers in the hour before dawn on the last day of provisioning recordings (day 12 or 13 of the breeding attempt). We avoided capturing the dominant male by first checking the focal bird's vent mark (see above for marking; the birds' vents are visible from below while they roost in their sleeping chambers). Dominant females, who roosted inside the breeding nest, were not disturbed either. Caught subordinate birds were then kept in individual cages following approved ethical guidelines (University of Pretoria Animal Ethics Committee EC007-17) until the end of provisioning data collection 4 hours after sunrise, when the caught subordinates were released onto their territories. Observations confirmed that these birds always reintegrated into their groups. In control treatment groups, at dawn on the last day of provisioning recordings (day 12 or 13 of the breeding attempt), subordinates were not caught and caged; instead, the experimenter (P.C.-L.) walked underneath the roosting

tree (as one does when catching the birds) to expose the dominants to a similar disturbance to that experienced by dominants in removal groups. This approach yielded $n = 11$ complete removal treatments and $n = 16$ complete control treatments (the difference in sample size arose because not all helpers were successfully caught in five of the intended removal broods).

First, we investigated the effect of the treatment (complete helper removal versus control) on the change in the total provisioning rate between the day of experimentation and the previous (unmanipulated) provisioning day for the same brood. No broods changed in size between the two focal days, and brood sizes did not differ between the two treatment groups (t test: $N_{\text{control}} = 16$, $N_{\text{removal}} = 11$, $t = -0.53$, $df = 25$, $P = 0.602$). Likewise, the total duration over which provisioning behavior was recorded did not differ (i) between the two focal days for each brood (t test: $t = 0.29$, $df = 26$, $P = 0.771$) or (ii) between the treatment groups (t test: $t = 0.48$, $df = 25$, $P = 0.635$).

Second, we conducted a sex-specific analysis of these experimental data to corroborate our correlative finding that the number of female helpers has a stronger effect on the total rate at which broods are fed than the number of male helpers [see Results and Discussion and Fig. 1 (D to F)]. To test whether the removal of all female helpers affected the within-brood change in total provisioning rate relative to the previous day, we compared the change in provisioning rate for (i) broods in which all female helpers were removed ($n = 7$ broods) versus (ii) broods in which no female helpers were removed ($n = 20$ broods), while controlling for a possible effect of the number of male helpers removed. To then test whether the removal of all male helpers affected the within-brood change in total provisioning rate, we compared the change in provisioning rate for (i) broods in which all male helpers had been removed ($n = 8$ broods) versus (ii) broods in which no male helpers were removed ($n = 19$ broods), while controlling for a possible effect of the number of female helpers removed.

Rainfall data

Daily rainfall data for the area where our study population is located were collected from two rainfall gauges located to the west ($27^{\circ}16'58.9''\text{S}$, $22^{\circ}23'02.1''\text{E}$) and east ($27^{\circ}17'42.1''\text{S}$, $22^{\circ}27'34.9''\text{E}$) of our study site, 7.60 km apart. These two rainfall measurements were highly correlated during the study period (Pearson's product-moment correlation: $r = 0.875$, 95% CI = 0.867 to 0.882, $df = 3,347$). We, therefore, calculated average daily values across both gauges and used this as a proxy for rainfall conditions at our study site.

Statistical analysis

General modeling approach

All statistical models and visualizations were carried out in R (version 3.5.1 to 3.6.1) (33). The importance of single predictors and statistical hypotheses (e.g., a given combination of model predictors) in univariate models was assessed using an information-theoretic approach. Starting from a global model, containing every predictor and interaction of interest, simpler models containing combinations of fixed predictors were fitted to the data and these different models were ranked on the basis of AIC (34). Linear mixed models compared by AIC were fitted using maximum likelihood. ΔAIC values were then calculated for every model (i.e., the difference in AIC between the focal model and the best-supported "top" model). As lower AIC values are indicative of stronger statistical support, the ΔAIC for the top model = 0 and models that attracted less statistical support had progressively more positive ΔAIC values.

We gave consideration to models within a Δ AIC value of six (35) and subsequently reduced this Δ 6 “top-model set” by applying the “nesting rule” described in (35). This rule aims to avoid the retention of overly complex models that do not improve model fit by discarding models that are more complex versions of simpler (nested) models with weaker AIC support (35, 36). Adding variables with little or no explanatory power to a top model can weaken AIC by less than 6 points, leading to the retention within the Δ 6 top-model set of more complex versions of better supported models, containing such uninformative variables (36). The nesting rule tries to reduce the chance of considering models with such uninformative variables (35). Every model set included intercept-only models. When quadratic terms were included in a given model, linear coefficients were always present. In the model selection tables, each line presents a model from the top-model set [i.e., those models within Δ AIC = 6 of the “top model” (the model with the lowest AIC)], while each of the fixed effect (predictor) columns presents the estimated effect size for that fixed effect in that model (or is blank if the focal fixed effect was absent from that model).

Addressing the potentially confounding effects of variation in maternal or territory quality in our analyses of helper effects: Experimental evidence and within-mother centering

A common concern in studies of cooperative species is that group size and helper numbers can be associated with maternal or territory quality, creating a spurious correlation between group size/helper number and reproductive output (both of which could be positively associated with maternal or territory quality) (37). We address this concern in three different ways. First, we show experimental evidence for a positive causal link between the number of female helpers and the total provisioning rate to the offspring. Second, we exclude young individuals from our calculations of the numbers of male and female helpers (as transient resource peaks leave recent and current productivity positively correlated, which could otherwise generate a spurious correlation between helper number and current productivity if recently produced young were also considered helpers). Third, we carry out our analyses first using the number of helpers as a predictor and then partitioning variation in the number of helpers into its within-mother and among-mother components [Δ helper number and μ helper number, respectively (38)]. “ μ helper number” is the average helper number that a mother had across all of her breeding attempts in the relevant dataset, whereas “ Δ helper number” is the difference between her helper number in the focal brood and μ helper number. This approach allows us to statistically isolate the effects on performance of within-mother (Δ) variation in helper number (which is both within-mother and within-territory, as each mother in our analyses only ever held one territory), in the knowledge that its effects cannot be attributed to variation in quality among mothers or their territories.

Analyses of provisioning rates

The sex difference in helper contributions to offspring provisioning (Fig. 1C) was demonstrated using a linear mixed model of helper provisioning rates (log+1 transformed to meet assumptions of normality), including date of observation, social group ID, brood ID, and helper ID as random intercept terms. Helper sex, brood size, and brood age were included as fixed effect predictors.

The effect of helpers on natural variation in the total provisioning rate to broods (Fig. 1, D and E) was analyzed using linear mixed models, including date of observation, social group ID, and brood

ID as random intercept terms. Number of female helpers, number of male helpers, brood age, and brood size were included as fixed effect predictors. To confirm that the detected relationships with helper numbers were not confounded by variation in maternal or territory quality, we then reran the modeling process following the partitioning of male and female helper numbers in to their within- and among-mother components (as outlined above).

Data from the removal experiment (see above for methodological details) was also analyzed using linear mixed models, including social group ID (which also captures brood ID in this dataset) and date of observation as random intercept terms. The response term for these models was the change in total provisioning rate to the brood between the morning of the treatment day (when the helpers had either been removed at dawn or not) and the morning of the preceding, unmanipulated, day. The analysis sought to assess whether the treatment [removal (the removal of all helpers) or control (the removal of no helpers)] affected the magnitude of this change. We therefore included treatment (removal or control) and brood age on the treatment day (either 12 or 13 days old) as fixed effect predictors. Having identified a clear effect of the removal of all helpers, we then sought to corroborate our correlative finding that the number of female helpers has a stronger effect on the total rate at which broods are fed than the number of male helpers (see experimental methods above for details and the sample sizes for this approach). First, we tested the effect of having removed all versus no female helpers, by again conducting a linear mixed model of the change in total provisioning rate from the previous day, now with the following fixed effect predictors: brood age, number of male helpers removed, and treatment (now, whether all or no female helpers were removed from the group). Second, we tested the effect of removing all versus no male helpers, using a similar approach but with the following fixed effect predictors: brood age, number of female helpers removed, and treatment (now, whether all or no male helpers were removed from the group).

Bayesian bivariate analyses of the effects of female helper number on the mean and variance in reproductive success of related breeders

A bivariate linear model (i.e., a model with two response terms) was used to simultaneously investigate the effects of helpers on both the mean and variance in reproductive success of mothers. By setting the two response terms to be the reproductive success of mothers in two different helping contexts (e.g., with no versus some helpers; see below for further details), this analytical approach allows formal comparisons to be made of the mothers’ mean and variance in reproductive success between the two contexts, thereby revealing the effects of helpers on each parameter. The mother’s mean reproductive success in each helping context is captured by the model’s estimate of the intercept for reproductive success in that helping context, while the mother’s variance in reproductive success in each helping context is captured by the models’ estimate of the residual variance in reproductive success in that helping context; see table S2 for an example model output. Thus, we could formally determine whether helping affected (i) the variance in reproductive success by assessing the strength of evidence that the residual variance differed between the two helping contexts (after controlling for the other fixed and random effects) and (ii) mean reproductive success by assessing the strength of evidence that the intercept differed between the two helping contexts (after controlling for the other fixed and random effects). While estimating covariances for random

effects across the two modeled contexts was not of primary interest, these were estimated and so are also reported in the full model tables (see model structure below and tables S2, S4, and S7).

In these bivariate models, we modeled reproductive success as the number of nestlings that fledged from a given breeding attempt while controlling for variation in the number of nestlings that hatched as a fixed effect predictor [as female helpers have a causal positive effect on the overall rate of nestling provisioning (Fig. 1) and, hence, the potential to affect nestling survival from hatching to fledging]. The number of fledglings was modeled using a Gaussian error distribution, as this allows the independent estimation of means and variances (these two parameters are coupled in other distributions). The two response terms were modeled allowing for independent intercepts (capturing mean reproductive success) and residual variances (capturing variance in reproductive success) across the two helping contexts. The models also included random effect variances (and covariances across the two helping contexts) for breeding season ID and mother ID.

We conducted two sets of these bivariate linear mixed models. First, to investigate the effect of having female helpers on both the mean and variance in reproductive success of mothers, we fitted a bivariate model in which the two response variables were the number of nestlings that fledged from (i) breeding attempts in which the mother had no female helpers (185 broods from 63 mothers) and (ii) breeding attempts in which the mother had some (i.e., one or more) female helpers (215 broods from 51 mothers). Forty-six dominant females had broods in both contexts. This first bivariate analysis revealed that mothers with female helpers showed lower (residual) variance in reproductive success than mothers with no female helpers (see main paper). To verify whether this effect holds when we explicitly examine the effect of within-mother variation in female helper number, we then (i) partitioned female helper number into its within-mother (Δ) and among-mother (μ) components (see above for partitioning method) and (ii) carried out a second bivariate linear mixed model in which the two response variables were now the number of nestlings that fledged from (i) breeding attempts in which within-mother (Δ) female helper number was less than or equal to zero [i.e., in the focal breeding attempt, the mother had fewer (or the same number of) female helpers than her own mean female helper number across all of her breeding attempts in the dataset; 227 broods from 56 mothers] and (ii) breeding attempts in which within-mother (Δ) female helper number was greater than zero (i.e., the mother had more female helpers than her own mean female helper number; 161 broods from 49 mothers). We excluded from this analysis any dominant females with only one breeding attempt in our dataset, and, hence, no within-mother variation in female helper number ($n = 12$ mothers).

We fitted the bivariate linear mixed models using the “MCMCglmm” R package (39), running two independent Markov chain Monte Carlo (MCMCs) of 210,000 iterations with an initial burn-in period of 10,000 iterations and a thinning interval of 100 iterations. MCMC effective sample size for every model estimate was always higher than 1000. We assessed the convergence of MCMC models by visualizing MCMC traces and calculating the Gelman-Rubin diagnostic (upper confidence interval < 1.01 in every case). Statistical assessments of the differences between model coefficients or variance components across contexts were conducted using the 95% credible interval for the difference between pairs of estimates. Default priors were used for fixed effects (normal distribution, $\mu = 0$, $\sigma^2 = 10^8$) and residual

variances (inverse Wishart, $V = 1$, $\nu = 0.002$). Parameter expanded priors were used for random (co)variances with $\mu_\alpha = 0$ and $\sigma_\alpha^2 = 25^2$. **Sliding window approach for rainfall effects on proportion of nestlings that fledged**

To investigate whether female helpers reduce variance in maternal reproductive success by specifically reducing rainfall-related variance in reproductive success, we first had to establish the temporal window over which fallen rain affects the success of a given breeding attempt. To do this, we used a sliding window optimization approach, considering all possible temporal windows of >4 days in length, between an earliest start date of 80 days before the estimated earliest date of fledging (18 days after hatching) and a latest end date of the estimated date of fledging. Only sliding windows of >4 days in length were considered, to decrease the likelihood of false-positive results (which are more probable for very short windows). For each rainfall window, the total amount of rainfall during the window was calculated for all breeding attempts in the dataset and then fitted as an additional predictor in a “baseline model” of nestling survival (see below for specifications) to test the explanatory power of that rainfall window. The AIC of this model was then compared to the AIC of the baseline model before the inclusion of the rainfall predictor, yielding a Δ AIC value (“AIC support”). We allowed for both linear and quadratic rainfall effects. The Δ AIC values for all of the different rainfall windows were then ranked, and the best-supported rainfall window was chosen (for use in our analysis of rainfall-dependent helper effects; see next section). As several factors may compete with rainfall to explain variation in nestling survival, the explanatory power of the different rainfall windows were assessed by adding each rainfall predictor to the following baseline model: a binomial mixed model of the proportion of nestlings that survived to fledging, which included breeding season ID and mother ID as random effects, alongside the following fixed effects—number of female helpers, number of male helpers, brood size, number of female helpers \times brood size, and number of male helpers \times brood size.

To assess the likelihood that this sliding window approach yielded a false-positive result for the best rainfall window, we carried out 10 randomizations of the dataset. In each randomization, the “biological reference date” (in this case, the focal brood’s estimated earliest date of fledging; see above) in the dataset was randomized by reshuffling, similar to the approach implemented in the R package “climwin” (40). Following each randomization of the dataset, the full sliding window protocol above was applied and the distributions of AIC support for the different rainfall windows were recorded. We then verified that the best-supported rainfall window identified using the real (nonrandomized) dataset attracted stronger AIC support than the best-supported rainfall window in every one of the 10 AIC distributions that arose from applying the sliding window approach to the randomized datasets.

Modeling the effects of rainfall and female helper number on nestling survival

To investigate whether female helpers specifically reduce rainfall-related variance in maternal reproductive success, we used a binomial mixed model of the proportion of nestlings that survived to fledging (“nestling survival”) to test for the required interaction between female helper number and rainfall (the total rainfall during the focal window identified to best predict nestling survival; see previous section). The initial “global” model contained all of the fixed and random effects used in the baseline model used in the sliding window approach (see previous section), as well as the total amount

of rainfall calculated for the best-supported rainfall window (“rainfall” hereafter) and the two-way interactions between rainfall and both the number of female helpers and the number of male helpers. This global model was not overdispersed (residual deviance = 668.82, $df = 383$), and a simulation of scaled model residuals, using the R package “DHARMA” (41), suggested a uniform distribution of model residuals (500 model simulations; Kolmogorov-Smirnov test, $D = 0.057$, $P = 0.156$). The global model was, then, subjected to AIC model selection (as outlined above). To then confirm that the detected interaction between female helper number and rainfall was not confounded by variation in maternal or territory quality, we repeated the model selection process following the partitioning of female helper number in to its within- and among-mother components (as outlined above).

Effects of rainfall on the absolute probability of predation and starvation

To shed light on the mechanisms that may leave rainfall affecting the helper effects in this population (Fig. 3), we used the circumstances surrounding the disappearance of nestlings to infer a probable cause of death (predation or starvation) and then conducted analyses of the effect of rainfall on the absolute probabilities of predation and starvation. As we were better able to characterize the likely cause of death within broods of two nestlings (see below; the modal brood size), we focused these analyses solely on broods of two nestlings ($n = 232$ broods by 61 mothers).

The “predation” or “starvation” fates were assigned to entire broods according to the following definitions. Predation was considered the likely cause of mortality for broods (i) when signs of predation were present (mongooses, genets, and goshawks are common predators of white-browed sparrow-weaver broods, and they leave visible damage to the nest structure that is associated with the disappearance of the entire brood) or (ii), in the absence of evident nest damage of any kind (as damage may rarely occur under predation by snakes), when both nestlings in a brood disappeared in the same interval between successive nest checks (i.e., within 4 days of each other) despite appearing healthy when last checked. Starvation was considered the likely cause of mortality within a brood whenever one nestling died during a given nest-check interval (most often the lightest individual), while its sibling survived that same nest-check interval (regardless of this sibling’s downstream fate). As both definitions required information from our regular nest checks (which cease when broods are 17 days old, to avoid pre fledging older broods), these predation and starvation fates were only assigned to broods up to the age of 17 days. Mortalities that occurred between 17 days of age and fledging were therefore not assigned fates in these analyses.

We fitted two binomial generalized linear mixed models to investigate the effect of total rainfall on (i) the absolute probability of whole-brood predation and (ii) the absolute probability that the brood experienced starvation. Total rainfall during the brood’s focal window (as calculated in the sliding window analysis for offspring survival; see above) was fitted as a fixed effect predictor. Mother ID, social group ID, and breeding season were included as random intercepts. To ensure that we were examining the impact of rainfall on the patterns of nestling mortality over the same rainfall range considered in our analyses of rainfall-dependent helper effects [e.g., Fig. 3; which focused on the total rainfall range that reflects an ecological continuum between harsh and benign conditions (0 to 185 mm; see Supplementary Materials D)], we restricted these

analyses of mortality causes to the 200 two-nestling broods for which total rainfall was <185 mm. Repeating these analyses using all two-nestling broods reared in all rainfall conditions (i.e., all $n = 232$ broods) yielded similar results (see fig. S3 for details).

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <https://science.org/doi/10.1126/sciadv.abe8980>

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Altruistic bet-hedging and the evolution of cooperation in a Kalahari bird

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