Evolution of sex differences in cooperation: the role of trade-offs with dispersal

Pablo Capilla-Lasheras[1, 2, #], Nina Bircher[3], Antony M. Brown[1], Xavier Harrison[1], Thomas Reed[4], Jennifer E. York[5,6], Dominic L. Cram[5], Christian Rutz[7], Lindsay Walker[8], Marc Naguib[3], Andrew J. Young[1, #]

[#] Corresponding authors: PC-L, AJY
Email: pacapilla@gmail.com / A.J.Young@exeter.ac.uk

[1] Centre for Ecology and Conservation, University of Exeter, Penryn, UK
[2] School of Biodiversity, One Health and Veterinary Medicine, University of Glasgow, Glasgow, Scotland
[3] Behavioural Ecology Group, Wageningen University & Research, Wageningen, The Netherlands
[4] School of Biological, Earth and Environmental Sciences, University College Cork, Cork, Ireland
[5] Department of Zoology, Downing Street, University of Cambridge, Cambridge, UK.
[6] Department of Zoology and Entomology, University of Pretoria, Pretoria, Republic of South Africa
[7] Centre for Biological Diversity, School of Biology, University of St Andrews, Sir Harold Mitchell Building, St Andrews, UK
[8] Psychology, Washington Singer Building, University of Exeter, Exeter, UK

Keywords: cooperation, sex differences, philopatry, dispersal, radio-tracking.

Abstract

Explaining the evolution of sex differences in cooperation remains a major challenge. Comparative studies highlight that offspring of the more philopatric sex tend to be more cooperative within their family groups than those of the more dispersive sex but we do not understand why. The leading 'Philopatry hypothesis' proposes that the more philopatric sex cooperates more because their higher likelihood of natal breeding increases the direct fitness benefits of natal cooperation. However, the 'Dispersal trade-off hypothesis' proposes that the more dispersive sex cooperates less because preparations for dispersal, such as extra-territorial prospecting, trade-off against natal cooperation. Here, we test both hypotheses in cooperatively breeding white-browed sparrow weavers (*Plocepasser mahali*), using a novel high-resolution automated radio-tracking method. First, we show that males are the more dispersive sex (a rare reversal of the typical avian sex-difference in dispersal) and that, consistent with the predictions of both hypotheses, females contribute substantially more than males to cooperative care while within the natal group. However, the Philopatry hypothesis cannot readily explain this female-biased cooperation, as females are not more likely than males to breed within their natal group. Instead, our radio-tracking findings support the Dispersal trade-off hypothesis: males conduct pre-dispersal extra-territorial prospecting forays at higher rates than females and prospecting appears to trade-off against natal cooperation. Our findings thus highlight that the evolution of sex differences in cooperation could be widely attributable to trade-offs between cooperation and dispersal; a potentially general explanation that does not demand that cooperation yields direct fitness benefits.

Introduction

The evolution of sex differences in cooperation remains a major evolutionary puzzle (1–6). In many cooperatively breeding species, in which offspring of both sexes delay dispersal from their natal group and help to rear future generations of their parents' young, one sex contributes significantly more than the other to such cooperative care within the natal group (3, 4, 6–8). These sex differences in natal cooperation are of particular interest as they occur in the absence of sex differences in average relatedness to recipients (as helpers of both sexes are still residing within their natal groups), leaving it unlikely that kin selection alone can explain their evolution (1, 3–6). Recent comparative analyses have highlighted that, across cooperative breeders of this kind, sex differences in contributions to cooperative care while within the natal group are predicted by the species' sex difference in dispersal; resident offspring of the more philopatric sex tend to contribute to natal cooperation at higher rates than resident offspring of the more dispersive sex (5, 6). However, why the more philopatric sex contributes more to natal cooperation is not clear as the two major evolutionary explanations proposed for this pattern have not been teased apart (3–6, 9).

The leading hypothesis for the evolution of sex differences in natal cooperation, the 'Philopatry hypothesis', proposes that offspring of the more philopatric sex help at higher rates (while both sexes reside within the natal group) because, by staying in their natal group for longer they stand to gain a greater downstream direct fitness benefit from cooperation (1, 3, 5). This hypothesis therefore requires that cooperation yields a direct fitness benefit and that the accrual of this benefit is to some extent contingent upon remaining within the natal group. For example, the more philopatric sex may be more likely to ultimately breed within the natal territory and may thus stand to gain a greater downstream direct fitness benefit from cooperating to rear additional natal group members that may ultimately help them back (1–3, 5). A recent comparative study of the cooperative birds in which both sexes delay dispersal and help has found support for this idea (5); species with more female-biased probabilities of ultimately breeding within the natal group showed more female-biased helper contributions to cooperative care while within the natal group. These findings are consistent with the key prediction of the Philopatry hypothesis and could therefore constitute rare evidence that direct fitness benefits have played a widespread role in the evolution of helping behaviour (5; see also 9). However, these findings are also consistent with an alternative less-studied hypothesis which also predicts that the more philopatric sex should help more, regardless of whether helping yields a direct benefit; the 'Dispersal trade-off hypothesis'.

The Dispersal trade-off hypothesis proposes that offspring of the more dispersive sex help at lower rates (while both sexes reside within the natal group) because all individuals face a trade-off between investments in natal cooperation and activities that promote dispersal from the natal group, such as extra-territorial prospecting for dispersal opportunities (4, 9). Thus, while the Philopatry hypothesis requires that cooperation yields a downstream direct fitness benefit, the Dispersal trade-off hypothesis does not. In many social species offspring prepare for dispersal by conducting extra-territorial prospecting forays while still resident within their natal group (1, 4, 9, 11–14). These forays may yield information on dispersal opportunities and thus increase the likelihood of securing a breeding position elsewhere (1, 4, 13, 14). In some species, extra-territorial forays can also yield immediate fitness benefits by offering access to extra-group matings (12). Investments in prospecting could trade-off against natal cooperation because the two activities cannot be carried out at the same time, but also because costs and physiological changes associated with prospecting have the potential to reduce the expression of helping behaviour (9, 13, 15–17). Given the potential costs of helping (18, 19), frequent prospectors could also reduce their helper contributions to maintain competitive phenotypes that reduce the risks and/or increase the likely success of prospecting. However, little is known about prospecting in cooperative breeders due to the difficulty of monitoring the cryptic, fast and often long-distance movements that prospectors make (4, 9, 11, 13, 17). One study of male meerkats, *Suricata suricatta*, whose frequent extra-territorial forays yield extra-group matings (12), suggests that investments in such forays may indeed trade-off against natal cooperation (9). But whether prospecting for dispersal opportunities *per se* (which may occur at lower rates than mating forays and could entail different costs) can also trade off against natal cooperation is not known.

As the Philopatry and Dispersal trade-off hypotheses for the evolution of sex differences in cooperation *both* predict that helpers of the more philopatric sex should contribute to cooperative care within the natal group at higher rates (consistent with the findings of comparative studies (5, 6)), discriminating between them now requires innovative studies of individual model systems to test whether the different underlying processes assumed by each hypothesis are acting as required to explain the observed sex difference in cooperation.

Here, we combine long-term data on life-histories and cooperative behaviour with a high-resolution automated radio-tracking study of prospecting behaviour to test both the predictions and core assumptions of the Philopatry and Dispersal trade-off hypotheses (see below), using cooperatively-breeding white-browed sparrow weavers, *Plocepasser mahali*, as a model system. White-browed sparrow weavers (hereafter ‘sparrow weavers’) are cooperative birds that live in social groups which defend year-round territories across

the semi-arid regions of East and Southern Africa (20, 21). Within each group, a single dominant male and female monopolise reproduction and their offspring of both sexes delay dispersal, becoming non-breeding subordinates that cooperatively help to feed future generations of nestlings produced by the breeding pair (21, 22). As offspring of both sexes never breed within their natal group while subordinate (22), the only route to natal breeding is via inheritance of the natal dominant (breeding) position. The primary route to dominance for both sexes, however, is via dispersal to other groups (23). Dispersal is typically local in both sexes (23), but genetic analyses and field observations suggest that males disperse significantly further on average than females from their natal to breeding sites (23), and therefore that females are the more philopatric sex; a rare reversal of the typical avian sex-bias in dispersal (24). In this study, we establish whether there are also sex biases in the probabilities of becoming dominant within the natal group and of dispersal from the natal group (the dispersal traits most relevant to the focal hypotheses). Subordinates of both sexes conduct prospecting forays prior to dispersal from their natal group, which are commonly met with aggression from the holders of visited territories (23, 25, 26). The rarity of extra-group parentage by subordinates (<1% of paternity; (22)) suggests that the primary function of these forays is to promote dispersal.

Subordinate female sparrow-weavers cooperatively feed offspring at higher rates than subordinate males (27); a pattern rarely documented among birds (4). In this study, we establish whether this sex difference in cooperative contributions is also evident among subordinates within their natal groups (which is the focus of the focal hypotheses). Without focussing on natal subordinates, such a sex bias in cooperation could be attributable instead to kin selection: male-biased dispersal may leave the incidence of subordinate immigrants higher among males than females, and subordinate immigrant sparrow-weavers rarely help at all (23, 28), typically being unrelated to potential recipients (22). Helper contributions to cooperative care increase the overall rates at which nestlings are fed in this species (27), but do not appear to increase the average rate of nestling survival to fledging (27). Helping may instead yield indirect fitness benefits by reducing environmentally-induced variance in the reproductive success of related breeders (27), improving their survival (29) and enhancing the quality of their offspring (30). Helping could also conceivably yield direct fitness benefits, but as subordinate immigrants rarely help at all (28) it seems unlikely that these benefits are substantial (see discussion for more detail). Helping behaviour could, for example, yield a downstream direct fitness benefit to helpers if they inherited the dominant (breeding) position in their natal group and were then helped by offspring that they had previously helped to rear; a mechanism commonly envisaged in the Philopatry hypothesis (1, 5).

First, we demonstrate that the sex differences in dispersal and cooperation in sparrow-weaver societies satisfy the predictions of both the Philopatry and Dispersal trade-off hypotheses: this species shows a rare reversal of the typical avian sex biases in both dispersal incidence and natal cooperation. We then test for the underlying processes assumed by the Philopatry and Dispersal trade-off hypotheses to establish whether either hypothesis could credibly explain why this rare example of female-biased philopatry in birds is accompanied female-biased natal cooperation. Regarding the Philopatry hypothesis, we test whether female helpers are indeed more likely than males to inherit the breeding position within their natal group; the most commonly invoked mechanism by which the more philopatric sex could gain a greater downstream direct benefit from cooperation (3, 5). Regarding the Dispersal trade-off hypothesis, we use a high-resolution automated radio-tracking study of extra-territorial prospecting behaviour to test its two key assumptions: first, that male helpers (the more dispersive sex) conduct extra-territorial prospecting forays at higher rates (or over greater distances or for longer durations) than females; second, that investments in prospecting from the natal group trade off against concurrent investments in natal cooperative care.

Results

1. Testing the Predictions of the Philopatry and Dispersal trade-off Hypotheses

Consistent with the predictions of both focal hypotheses, sparrow weavers show a significant male-bias in dispersal incidence coupled with a significant female-bias in contributions to natal cooperation. From the 178 males and 160 females born in our study groups between September 2007 and April 2014 that survived to at least six months old, and whose dispersal movements were monitored until April 2016, 52 males and 30 females were observed to disperse from their natal group to become resident in another group, suggesting a male-biased incidence of dispersal from the natal group (2-sample test for equality of proportions: $\chi^2_1 = 4.47$, $p = 0.035$). This pattern was confirmed by modelling the age-specific probability of dispersal from the natal group: subordinate natal males are more likely to disperse than subordinate natal females across all age classes (Figure 1a, $\chi^2_1 = 9.64$, $p = 0.002$; Table S1). There was evidence that dispersal probability increased with age (Figure 1a, $\chi^2_3 = 64.98$, $p < 0.001$; Table S1), but no evidence that the sex difference in dispersal probability changed with age (sex x age interaction: $\chi^2_3 = 1.35$, $p = 0.717$; Table S1). The Philopatry and Dispersal trade-off hypotheses would therefore both predict that subordinate females (the more philopatric sex) should help at higher rates than subordinate males (the more dispersive sex) while within the natal group.

When modelling the contributions of subordinates within their natal groups to helping behaviour, subordinate females cooperatively fed broods at significantly higher rates than subordinate males (Figure 1b; $\chi^2_1 = 16.69$, $p < 0.001$; Table S2). Cooperative provisioning rates also increased initially with advancing age before decreasing slightly (Figure 1b; $\chi^2_3 = 27.41$, $p < 0.001$; Table S2), but there was no indication that the magnitude of the sex difference changed with age (sex x age interaction: $\chi^2_3 = 5.14$, $p = 0.162$; Table S2). Brood size and brood age both positively predicted cooperative provisioning rates ($\chi^2_1 = 11.58$, $p < 0.001$ and $\chi^2_6 = 26.16$, $p < 0.001$ respectively; Table S2). During their provisioning visits, subordinate females also spent significantly longer than subordinate males within the nest chamber (Figure 1c; $\chi^2_1 = 16.46$, $p < 0.001$; Table S3), and were just as likely as subordinate males to provision nestlings with food items that were large (Figure 1d; $\chi^2_1 = 1.43$, $p = 0.231$; Table S4). These sex differences in the cooperative provisioning rates of subordinates within the natal group occurred in the absence of sex differences in their relatedness to the nestlings fed (Figure 1e; $\chi^2_1 = 0.16$, $p = 0.691$; Table S5).

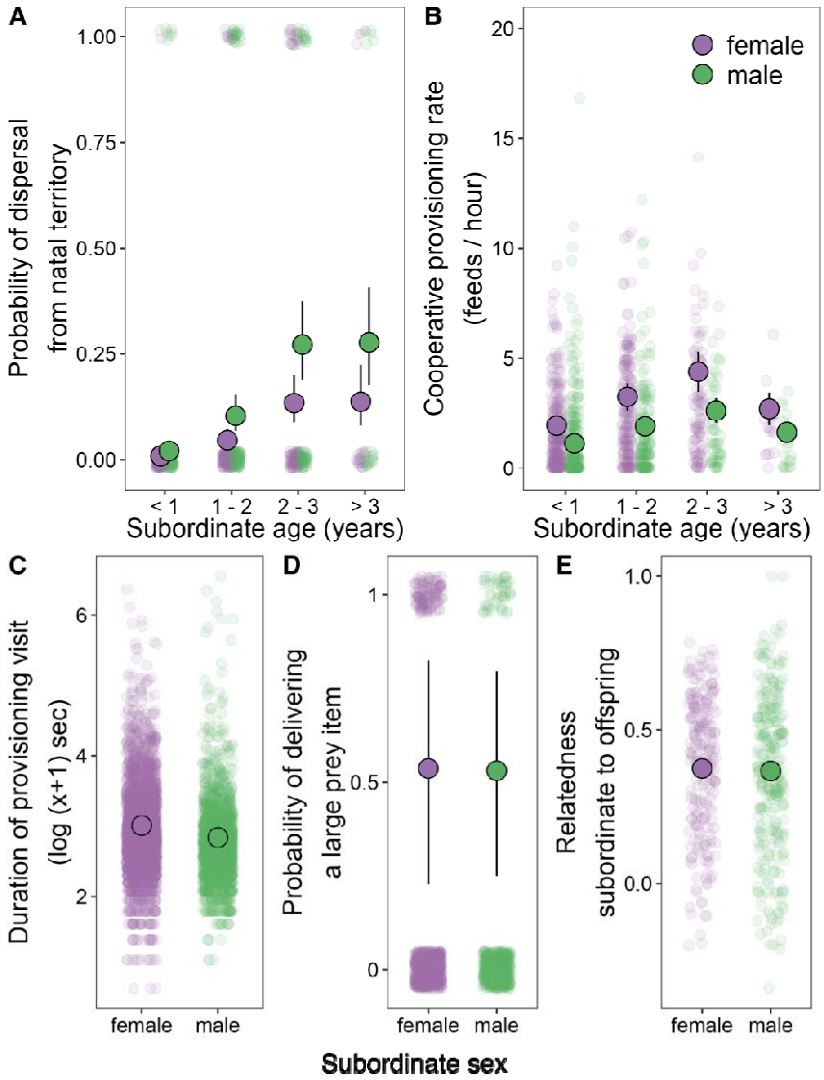

Figure 1. **Sparrow-weavers show a rare reversal of the typical avian sex differences in dispersal and natal cooperation. (a)** Among subordinate birds residing within their natal groups, males (green points) showed significantly higher age-specific probabilities of dispersal than females (purple points) (Table S1). (**b**) Among subordinate birds residing within their natal groups, females showed significantly higher cooperative nestling provisioning rates than males; a sex difference that did not vary with age (Table S2). (**c**) Natal subordinate females also spent significantly longer in the nest per provisioning visit than males (Table S3), and (**d**) were just as likely as natal subordinate males to feed the nestlings with food items that were large (Table S4). (**e**) These sex differences in natal helping behaviour were apparent in the absence of a sex difference in relatedness to the nestlings being fed (Table S5). Translucent points represent raw data whereas larger points and error bars give mean model predictions ± 1 SE.

2. Testing the Mechanisms Invoked by the Philopatry Hypothesis

While females show lower age-specific probabilities of dispersal from their natal group than males (Figure 1a), they were no more likely than males to obtain a dominant breeding position within their natal group (Figure 2; for all focal age classes of natal subordinates $\chi^2_1 < 0.65$, $p > 0.779$; Table S6-S9). For natal subordinates under 3 years of age, the probability of ultimately becoming dominant within the natal group was low (<10% on average; Figure 2) and showed no sex difference, yet sex differences in natal cooperation were clear at these ages (Figure 1b). Once subordinates reached 3 years of age within their natal group their probability of inheriting a natal dominance position markedly increased (to ~ 25%), but their contributions to natal cooperation significantly decreased at this age (Figure 1b). If we also included in these 'natal dominance acquisition' events any dominant breeding positions acquired *outside* the natal group by founding a new group within territory previously held by the natal group (i.e., territorial budding (1)), we still found no evidence of a sex difference in the probability of inheriting a natal dominant breeding position in any age class (Table S10-13).

There was also no significant difference between males and females in the proportion of all dominance acquisition events in stablished groups that occurred within the natal group (7 natal dominance acquisitions out of a total of 32 dominance acquisitions for males; 9 natal out of a total of 32 for females; 2-sample test for equality of proportions: $\chi^2_1 = 0.08$, $p = 0.773$); in *both* sexes dominance was typically acquired via dispersal to other groups. These similarly low probabilities of inheriting natal dominance for both sexes likely reflect the similar rarity of opportunities to inherit natal dominance for both sexes, given the low and comparable frequencies of dominance turnovers in both sexes: dominance tenures are relatively long and do not differ in mean length between the sexes (mean ± S.E.: males = 2.62 ± 0.32 years, range 0.18 – 5.84 years; females = 2.51 ± 0.33 years, range 0.16 – 7.51 years; Table S14). The observed sex difference in the age-specific probability of dispersal from the natal group (Figure 1a), likely reflects a sex difference in the *strategy* used to acquire dominance via dispersal, rather than the *incidence* of acquiring dominance via dispersal. Males were more likely than females to disperse from their natal group into non-breeding subordinate positions in other groups (46 of 56 observed natal male dispersals; 19 of 32 observed natal female dispersals; $\chi^2_1 = 4.16$, $p = 0.041$; Table S15), where they might ultimately win dominance or disperse again (23). But when females did disperse from their natal groups, they were more likely than males to disperse directly into dominant positions in other groups (10 of 56 dispersals for males; 13 of 32 dispersals for females; $\chi^2_1 = 4.16$, $p = 0.041$; Table S16).

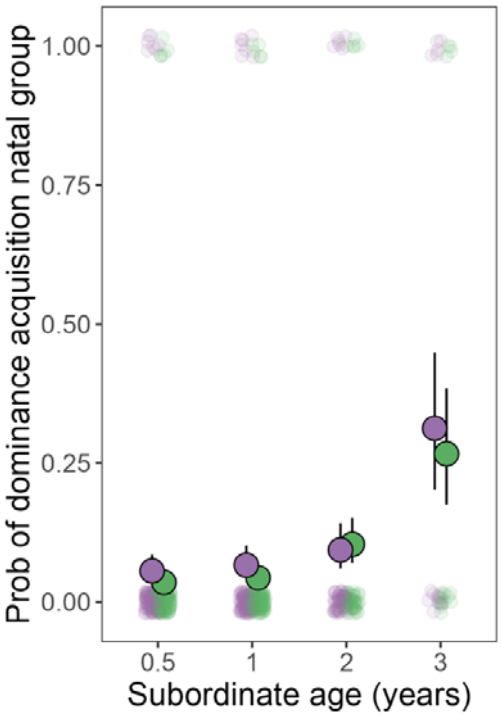

Figure 2. Age-specific probabilities of inheriting a dominant breeding position within the natal group, for subordinates still residing within their natal group at various ages. Subordinate females (purple points; the more cooperative sex; Figure 1b) were no more likely to inherit a breeding position within their natal group than subordinate males (green points; Table S6-S9). Our analysis focussed on subordinates within their natal group at a given focal age and tested for an effect of sex on their probability of inheriting a dominant breeding position within the natal group at some later time. The solid points show the sex-specific means (± SE) for subordinates of the focal age class, and the translucent points represent raw data. Subordinates were only included in the analysis if dominance turnovers were monitored within their focal group for a minimum of 2 years after the date on which the subordinate reached the focal age.

3. Testing the Mechanisms Invoked by the Dispersal Trade-off Hypothesis

Direct observations of prospecting behaviour

On 678 occasions, birds were observed visiting groups in which they were not resident. These individuals were often chased by birds within the visited territory (187 of 678 visits; 27.6%), hampering identification. But we did identify the visitor in 293 visits, and in 184 (62.8%) of these they were known to be subordinates resident in another group, who must therefore have been prospecting. Of these 184 prospecting forays by subordinates, 115 (62.5%) were conducted by 68 males and 69 (37.5%) were conducted by 51 females. These observations suggest male-biased prospecting behaviour given the approximately equal adult sex ratio in our population (115 of 184 forays is a significant deviation from 50%; Binomial test $p < 0.001$). However, such a sex difference could reflect a sex difference in the conspicuousness of prospectors to observers (or the ease which they could be identified), due to variation in the behaviour of prospectors and/or resident birds. We therefore used an automated radio-tracking technology, Encounternet (31, 32), to

provide continuous high-resolution information on prospecting movements for the first time in a cooperative bird (Figure 3a).

Automated tracking of prospecting behaviour

We deployed an array of 35 radio receivers (base-stations) across our study area (Figure S1) to track the prospecting forays of 27 radio-tagged subordinate adults (13 males and 14 females) living within their natal groups between February and April 2017. The tags were fitted with a leg-loop harness and the combination weighed just 1.2g (2.8% of the mean body mass of the tracked birds). The main body of the tag rested on the bird's lower back between the wings and the antenna passed down the tail (Figure 3a). Birds were tracked for an average of 37 days (range = 11–59 days) generating a total of 22,518,022 detection logs (individual base-stations log all tags within detection range every 5 seconds). After processing the data (see Methods), we detected a total of 971 extra-territorial prospecting forays. We used a conservative approach to identify extra-territorial forays: events in which our best estimate of the focal bird's location was >250m from the centre of the bird's own territory (at which there was always a radio receiver), continuously for >15 seconds. As the mean ± S.E. distance between neighbouring territory centres is just 93.7 m ± 4.56 m in our study population, these would typically have been prospecting movements beyond the territories of neighbouring groups; see Methods; Figure S1). This approach will minimise the chance that a resident bird's interactions with its neighbours are falsely interpreted as extra-territorial prospecting, but is likely to underestimate the true incidence of forays by excluding more local prospecting activity. The 971 forays principally occurred between 06:00h and 19:00h, with frequencies peaking in the cooler periods towards the start and end of the day (Figure 3b). The tagged bird's daily rates of prospecting varied widely from 0 to 26 forays per day (n = 895 daily rate measures from 27 tagged birds; mean = 1.09 / day; median = 1 / day). Forays had a mean duration of 18.59 minutes (median = 5.67 minutes; range = 0.42 – 493 minutes; Figure 3c). Our estimate of the distance travelled on each foray had a mean of 720.74 m (median = 647.60 m; range = 502.29 – 2026.15 m; Figure 3d). This too is likely to be an underestimate as our ability to detect longer distance forays was constrained by the spatial coverage of our receiver array (Figure S1) and because this estimate was calculated as twice the straight line distance to the bird's furthest estimated location on the array during its foray, but the birds could have taken a more complex path (see methods).

Consistent with our observations of prospector visits above, subordinate males showed significantly higher daily rates of prospecting from their natal groups than subordinate females (Figure 3e; $\chi^2_1 = 5.39$, $p = 0.020$; Table S17); this effect was consistent across different choices of distance threshold to detect forays; Figure

S2b). Prospecting rates were modestly but not significantly lower during nestling provisioning periods (i.e., when cooperative care occurs) than at other times (Figure 3e; $\chi^2_1 = 2.15$, $p = 0.142$; Table S17; this effect was also consistent across different choices of distance threshold to detect forays; Figure S2c). The magnitude of the sex difference in prospecting rate was not affected by whether the bird's social group was provisioning nestlings at the time (sex x provisioning interaction: $\chi^2_1 = 0.97$, $p = 0.324$; Table S17). There was no evidence of an effect of subordinate sex (or nestling provisioning periods) on either the duration ($\chi^2_1 = 0.08$, $p = 0.773$; Table S18) or estimated distance of individual forays ($\chi^2_1 < 0.01$, $p = 0.970$; Table S19). Older subordinates conducted shorter forays ($\chi^2_1 = 3.95$, $p = 0.047$; Table S18) but age did not predict prospecting rate ($\chi^2_1 = 0.23$, $p = 0.631$; Table S17) or the maximum distance travelled ($\chi^2_1 = 0.14$, $p = 0.708$; Table S19).

Focussing on 13 radio-tagged subordinates (6 males and 7 females) whose forays were tracked through a nestling provisioning period, we found evidence suggestive of a trade-off between prospecting and cooperative provisioning behaviour. An individual's prospecting rate over the three-day window prior to us quantifying individual contributions to cooperative nestling provisioning negatively predicted its cooperative provisioning rate (Figure 3f; $\chi^2_1 = 30.91$, $p < 0.001$; Table S20). We found no evidence that either the intercept or gradient of this apparent trade-off regression line differed between the sexes (sex effect on provisioning rate while accounting for prospecting rate: $\chi^2_1 = 1.39$, $p = 0.238$; sex x prospecting rate interaction; $\chi^2_1 = 0.52$, $p = 0.472$; Table S20), though the sample size for this comparison was small. The existence of a negative correlation between prospecting and cooperative provisioning rates was robust to the choice of time window over which we calculated prospecting effort (Figure S3).

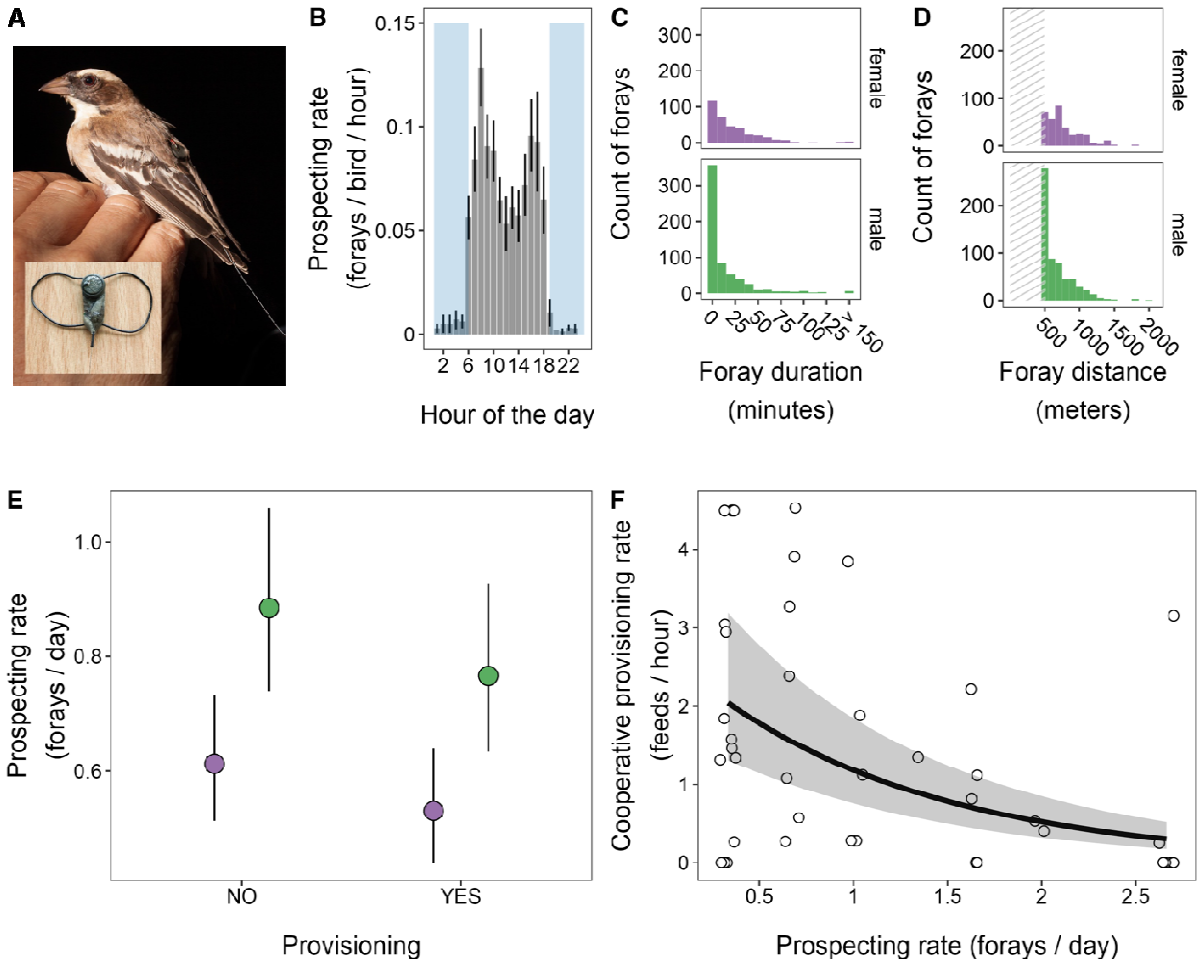

Figure 3. Extra-territorial prospecting behaviour and its trade-off with cooperation. (**A**) A subordinate female (females have pale bills) fitted with a radio-tag (pictured inset). The tag is fitted with leg loops and sits on the bird's lower back, where it is visible in the picture among the feathers. The aerial can be seen sitting along the tail feathers. (**B**) Circadian variation in prospecting behaviour; mean hourly prospecting rates per bird per hour of the day (mean ± 1 SE; from the 27 radio-tracked birds). The shaded area illustrates night hours (using as an approximation the civil twilight time for our study site on March 11th 2017 [06:05 and 19:14 hours], the date in the middle of our 6-week long prospecting study). The rare instances of forays at night could reflect birds being flushed from their roost chambers by predators. (**C**) Histogram of individual foray durations (nine observations, six for males and three for females, were clustered in '> 150' to help visualisation) and (**D**) distance travelled per individual round foray from the 27 radio-tracked birds. The 500m distance cut-off (striped area) reflects a conservative approach to defining forays, to rule out misclassifying interactions with neighbours (whose traits could be assessed anyway without prospecting). (**E**) Subordinate males have a significantly higher daily prospecting rate than subordinate females, both inside and outside peak periods of cooperative nestling provisioning (Table S17). (**F**) Individual variation in prospecting rate negatively predicted cooperative provisioning rate for the 13 radio-tagged birds (with repeated measures per individual) with prospecting data during a nestling period (Table S20). There was no evidence of a sex difference in the intercept or gradient of this regression line (Table S20). Mean model predictions ± 1 SE are illustrated in E and F.

Discussion

Our findings reveal that white-browed sparrow weavers show a rare reversal of the typical avian sex difference in dispersal (24). Males show higher age-specific probabilities of dispersal from their natal group than females and both population genetic analyses and observed dispersals suggest that males disperse further on average than females from their natal to breeding sites (23). Undetected longer-distance dispersals (beyond the bounds of our study site) may also be more common among males, as the low rate of immigration into our study population also shows a male bias (23). Both the Philopatry and Dispersal trade-off hypotheses for the evolution of sex differences in cooperation would therefore predict that sparrow-weavers should show female-biased natal cooperation, and our findings confirm this prediction. Natal subordinate females helped to feed nestlings at higher rates than natal subordinate males across the age classes, and spent longer within the nest on their feeding visits. This coupling of rare reversals of the typical avian sex biases in both dispersal and cooperation provides novel support for the predictions of the focal hypotheses, which are otherwise difficult to test given the limited variation in dispersal sex biases within taxonomic classes (4–6). Below, we consider the potential for the Philopatry and Dispersal trade-off hypotheses to account for the evolution of female-biased natal cooperation in this species, drawing on our empirical tests of the underling mechanisms assumed by each, and attend to potential alternative explanations. Our novel findings suggest that the mechanisms envisaged in the Philopatry hypothesis are unlikely to be acting in this species, and that the evolution of female-biased cooperation can be more readily explained by the mechanisms envisaged in the Dispersal trade-off hypothesis. We then consider the wider implications of this finding for our understanding of the evolution of sex differences in cooperation and, more broadly, the role that direct fitness benefits have played in the evolution of helping behaviour across cooperative breeders.

Among the diverse hypotheses proposed for the evolution of sex differences in cooperation (2, 6), the Philopatry and Dispersal trade-off hypotheses are unusual in predicting the evolution of female-biased natal cooperation in sparrow-weaver societies; alternative hypotheses cannot readily explain these patterns. That sex differences in natal cooperation occur here in the absence of a sex difference in relatedness to recipients implicates a central role for mechanisms other than kin selection in their origins (3, 5, 6). The heterogamety hypothesis (2, 6, 33) proposes that effects of the sex chromosomes on patterns of genetic relatedness could leave the heterogametic sex (females in birds) less cooperative, yet we see the opposite pattern here. Similarly, the paternity uncertainty hypothesis (2, 6, 34) predicts male-biased cooperation when extra-pair paternity occurs, yet we see the opposite pattern here despite dominant males losing 12-18% of paternity to

other dominant males (35). The parental skills hypothesis (2, 6) proposes that the sex that invests most in parental care could contribute most to helping if (i) helping yields a direct benefit by improving parenting skills, and (ii) this benefit is larger for the sex that contributes most to parental care. This hypothesis could be relevant to sparrow-weavers as dominant females feed offspring at higher rates than dominant males (28). However, compelling evidence that helping improves parenting skills remains elusive (2, 36), and as immigrant subordinate sparrow-weavers rarely help at all (28), it seems unlikely that direct benefits arising via skills acquisition are a major driver of helping in this system. Notably too, in a comparative study of cooperative breeders in which both sexes delay dispersal and help, the three other bird species that show female-biased parental care do not show female-biased natal cooperation, and the two other bird species that show female-biased natal cooperation do not show female-biased parental care (6). It has also been suggested that the sex that shows higher variance in lifetime reproductive success (LRS) may invest more in helping given its lower chance of securing direct fitness by breeding (2, 37). However, male and female sparrow-weavers likely have very similar variances in LRS, as both sexes only breed as dominants and do so in socially monogamous pairs (22), showing no evident sex difference in dominance tenure length. If anything, competition for extra-group paternity among dominant males (35) may leave males with slightly higher variance in LRS than females, but this would lead to the prediction of male-biased natal cooperation, and we observe the reverse.

The Philopatry hypothesis proposes that offspring of the more philopatric sex contribute more to natal cooperation because, by staying in their natal group for longer, they may stand to gain a greater downstream direct fitness benefit from natal cooperation (1, 3, 5). The most commonly invoked mechanism by which the more philopatric sex could gain a greater downstream direct benefit from natal helping, is if they are more likely to ultimately breed in their natal group and thus to benefit directly from having helped to increase the size of the natal helping workforce (1, 3, 5). However, this mechanism cannot readily explain female-biased natal cooperation in sparrow weavers, as neither sex breeds within their natal group while subordinate (22), and subordinate females were no more likely than males to inherit a dominant breeding position in their natal group or on territory previously held by their natal group. Our findings also give cause to question whether helping in this species does yield a direct benefit contingent upon inheriting natal dominance. If it did, one might expect the markedly higher chance of inheriting natal dominance once subordinates reach three years old (Figure 2) to be accompanied by an increase in cooperation at this age, yet we observed the opposite (Figure 1b). This finding may instead reflect subordinates showing greater restraint from costly helping once they become credible contenders for dominance (38), highlighting the possibility that helping actually

decreases a sparrow-weaver helper's downstream direct fitness prospects, at least at some life stages (38). The relative rarity of dominance acquisition within the natal group for both sexes in this species is likely due in part to the long average dominance tenure lengths of both sexes (which will leave natal inheritance opportunities rare; see results) and the fact that dominance turnover events are contested by queuing subordinates across the local area (23). As subordinate males and females are equally likely to inherit natal dominance, the observed male-bias in age-specific probability of dispersal from the natal group appears to reflect a sex difference in the *strategy* used to acquire dominance via dispersal, rather than in the *incidence* of acquiring dominance via dispersal; males disperse more frequently than females but employ a more complex strategy often involving staging as a subordinate in other groups, while females are more likely to disperse directly into dominance elsewhere; see results.

A second mechanism by which the more philopatric sex could conceivably gain a greater downstream direct benefit from natal helping (regardless of whether they inherit natal dominance), is if helping to rear offspring augments natal group size and if living in a larger group yields survival advantages to subordinates. Where this is the case, the more philopatric sex may enjoy this downstream direct benefit for longer because it will tend to remain in the natal group for longer (3). As female sparrow-weavers show lower age-specific dispersal probabilities than males, they are indeed likely to remain in the natal group for longer on average than males. However, this mechanism cannot readily account for female-biased natal cooperation in sparrow-weavers for two reasons. First, recent analyses of the long-term life-history data from our 40 study groups strongly suggest that subordinate sparrow-weavers suffer markedly *lower* survival rates in larger social groups (29). Thus, to the extent that helping does augment group size in this species, this mechanism is likely to leave females experiencing greater downstream direct fitness *costs* of helping, rather than benefits. Second, while both of the above mechanisms envisage that helping augments group size, helping may not actually augment group size in sparrow-weavers, as variation in helper numbers (whether female helpers, male helpers or both) does not positively predict either the rate at which dominant females breed (27) or the survival of their offspring to fledging (39, 40). Indeed, it seems unlikely that helping in sparrow-weaver societies yields an appreciable downstream direct benefit of any kind (e.g., via other conceivable mechanisms such as "pay to stay" or signalling "quality" (41–44)), as subordinates only help to rear offspring within their natal groups, where recipients are typically close kin (22, 28). While dispersers do integrate into other groups as immigrant subordinates where potential recipients are rarely kin (22), they virtually never help in this context (28); despite frequently acceding to dominance at some later date (23)). Together, our

findings suggest that the mechanisms envisaged in the Philopatry hypothesis cannot readily account for the evolution of female-biased natal cooperation in this species.

The Dispersal trade-off hypothesis proposes that the more dispersive sex contributes less to natal cooperation because all individuals face a trade-off between activities that promote dispersal (such as prospecting for dispersal opportunities) and natal cooperation (4, 9). It thus envisages that sex differences in cooperation arise not from a sex difference in the direct benefits of cooperation but instead from a trade-off between cooperation and other fitness-relevant traits in which sex differences exist. Our findings support the key prediction of the Dispersal trade-off hypothesis, that male-biased dispersal should be accompanied by female-biased natal cooperation, and provide evidence in support of the underlying mechanisms that it envisages. First, our automated radio-tracking study revealed that natal subordinates of both sexes prospect, but males (the more dispersive sex) prospect at significantly higher rates than females, while making forays of comparable duration and distance (though our ability to quantify longer distance movements was constrained by the scale of our tracking array). This male-bias in prospecting was also supported by our direct observations of prospectors visiting study groups. Subordinate males may benefit more from prospecting for dispersal opportunities than females because they are more likely than females to disperse in all age classes, and because they disperse further on average than females between their natal and breeding sites (23). While extra-territorial forays in some species function in extra-group mating (12, 45, 46), the forays of subordinate sparrow-weavers do not appear to serve this purpose (22, 35). That this male bias in prospecting was apparent during nestling provisioning periods highlights its potential to trade-off against cooperative care. That male-biased prospecting was also apparent *outside* nestling provisioning periods is important too, as this suggests that the sex difference in prospecting is unlikely to be a *product* of the sex difference in natal cooperation (i.e., a reversal of the causal direction suggested above), as it also occurs when subordinates are not engaged in cooperative care.

Our automated radio-tracking study also revealed support for the second key assumption of the Dispersal trade-off hypothesis: that investments in prospecting trade off against investments in cooperative care. Individuals that prospected at higher rates during nestling provisioning periods contributed significantly less to cooperative care. Consistent with the sexes facing a similar trade-off between prospecting and cooperation, and thus differing in their mean levels of cooperative care because they differ in their mean prospecting rates (the rationale of the Dispersal trade-off hypothesis), we found no evidence that this apparent trade-off regression line differed in either intercept or slope between males and females, though

our sample size for this comparison was small. The negative association between prospecting and natal cooperation cannot be readily attributed to uncontrolled variation among individuals in intrinsic ‘quality’, body condition or resource availability as these might be expected to generate positive among-individual covariance between resource-demanding traits, potentially obscuring, rather than generating, the negative association between traits that is expected of a trade-off (47).

As extra-territorial prospecting and cooperative care are both likely to entail energetic costs that may compromise body condition (9, 13, 19, 48) and induce oxidative stress (18), the observed negative association between prospecting and cooperation could reflect a simple resource allocation trade-off between the two traits (potentially mediated by endocrine changes associated with prospecting (9, 46)). While the extra-territorial forays of subordinate sparrow-weavers could well entail intense energetic expenditures, the total energetic costs entailed in active prospecting and any recovery from it might not be terribly high, as the more distant forays involving movements beyond neighbouring territories (the subset of forays studied here) occurred on average at modest daily rates and were often short in duration. However, prospecting is also likely to entail significant risks, as prospectors are frequently attacked when visiting other groups (4, 9, 13, 14) and could also face elevated predation risk while moving alone (17). As such, regular prospectors may stand to benefit more than others from maintaining a competitive phenotype, which could itself trade-off against costly cooperation, compounding the effects of any energetic and/or time costs entailed in conducting the actual forays. As both of these trade-off scenarios are consistent with the rationale of the Dispersal trade-off hypothesis, this hypothesis seems well placed to explain the evolution of female-biased natal cooperation in this species: males contribute less to natal cooperation because male-biased dispersal leaves them prospecting more, and all individuals face a trade-off between prospecting and natal cooperation. Further light may therefore be shed on the evolution of female-biased natal cooperation in this species by attempts to establish why this species has evolved its male-biased pattern of natal dispersal.

More than four decades ago, researchers of cooperative birds recognised that sex differences in cooperation could evolve because members of the more philopatric sex may stand to gain a greater downstream direct benefit from natal cooperation (1); the ‘Philopatry hypothesis’ here. The evidence that has accrued since is broadly consistent with this idea: the more philopatric (or less dispersive) sex tends to contribute more to helping while within the natal group, both in individual model systems ((3, 4, 7); and here) and across cooperative taxa in which both sexes delay dispersal and help (5, 6). However, the less-studied Dispersal trade-off hypothesis also predicts this pattern (4, 9), highlighting the need to now tease the two hypotheses

apart. Our findings suggest that the mechanisms envisaged in the Dispersal trade-off hypothesis are better placed to explain the evolution of female-biased natal helping in sparrow-weaver societies than those envisaged in the Philopatry hypothesis (see also (4)). This is important because, while both hypotheses could explain why sex differences in philopatry and dispersal predict sex differences in natal cooperation across taxa (5, 6), the Dispersal trade-off hypothesis could apply more widely, as it does not require that cooperation yields a downstream direct benefit contingent upon remaining in the natal group. The mechanisms envisaged in the Philopatry hypothesis could apply in species in which helping augments group size and in which group augmentation yields a downstream direct benefit to helpers while they delay dispersal (e.g., Florida scrub jays, *Aphelocoma coerulescens* (1)and meerkats, *Suricata suricatta* (3)). Indeed, these mechanisms may act in concert with those envisaged in the Dispersal trade-off hypothesis to select for sex differences in cooperation in such species (as both examples also show sex differences in helper prospecting (1, 9, 12)). But our findings highlight the need for caution when extrapolating the Philopatry hypothesis to species in which such mechanisms for the differential accrual of downstream direct benefits have yet to be demonstrated. On balance, it seems likely that the mechanisms envisaged in the Philopatry and Dispersal trade-off hypotheses have *both* played a role in the evolution of sex differences in natal cooperation across taxa, but that their relative importance may vary markedly among species.

Our findings have wider implications too for the role that direct benefits may have played in the evolution of cooperation. Recent comparative studies have reported that the probability that helpers will ultimately breed within their natal group predicts helper contributions to cooperative care across taxa; both their mean contributions relative to parents (10) and sex differences therein (5). These findings could constitute rare evidence that *direct* fitness benefits of helping have played a widespread role in the evolution of helping behaviour, alongside kin selection (5, 6, 10). However, our findings highlight that such associations could also arise in the absence of direct benefits of helping, via trade-offs between dispersal and cooperation: helpers with higher probabilities of natal inheritance might generally contribute more to natal cooperation across taxa because they need not invest as much in preparations for dispersal. Thus, while direct benefits of cooperation may indeed be important in some contexts, how widespread a role they played in the evolution of helping behaviour across taxa would seem to remain an open question.

Methods

Study system and life-history monitoring

This work was conducted as part of the long-term field study of white-browed sparrow weavers in Tswalu Kalahari Reserve in the Northern Cape Province of South Africa (27°16'S, 22°25' E). Fieldwork was carried out from September to May between 2007 and 2016 inclusive. All social groups within a study area of approximately 1.5 km^2 were monitored each year; approximately 40 groups, each defending a small year-round territory. Throughout the study period, all birds in the study population were fitted with a single metal ring, three colour rings for identification (under SAFRING license 1444) and genotyped using 10 microsatellite loci (see Supplementary Text A in (27) and (22) for genotyping protocols and relatedness calculations). The birds could be reliably caught from their woven roost chambers at night using custom-made sweep nets, and were then returned to their chambers to pass the remained of the night on completion of any processing. Social groups were easily distinguishable as all group members foraged together within their territory, defended it against neighbouring groups, and roosted within woven chambers in a single tree or cluster of trees close to the territory centre (22, 49). Each sparrow weaver group contains a single dominant (reproductive) pair and a variable number of non-breeding subordinates (22). Dominants are easily distinguished from subordinates because they display a distinct set of behaviours (49), and the sexes are easily distinguished after the first six months of life because the sub-species that we study (*P. mahali mahali*) exhibits a beak colour sexual dimorphism (50). Group compositions were assessed every week in the morning throughout each field season (27), and were confirmed by periodic captures of all group members from their roost chambers at night. We also sought to confirm the dominance status of birds on all such visits. Once a bird acquired a dominant position they retaining dominance for life. Dominance tenures typically ended with the bird's immediate disappearance from the study population; a scenario that likely reflects their death, given the very local nature of dispersal in this species and the relative rarity with which unmarked adults enter our study population from outside (23). On rare occasions dominants did transfer into a dominant position in another group, but on no occasion was a dominant bird known to subsequently become subordinate (either in their own group or any other). Dispersal was deemed to have occurred when an individual that was previously resident in one group (i.e., foraging with the group in the day and roosting on their territory at night) transferred to become resident in another group. All offspring delaying dispersal from their natal group and those that do disperse typically make just one or two dispersal movements in their lifetimes (22, 23). During our field observations from October 2011 onwards, we also noted any visits to groups by birds that were currently resident in other groups (i.e., prospecting birds) were also noted. Wherever possible we noted the colour-ring combinations of these prospecting birds, but aggression from

the territory residents often left this impossible (see results). Throughout each field season, we also checked every territory for nests (conspicuous woven structures with a different shape to roosting chambers) every one or two days, and wherever nests were present we check them for the presence of newly laid eggs. When new eggs were found we monitoring egg laying through to clutch completion and the fate of the brood through to fledging (22).

Quantifying the contributions of natal subordinates to cooperative provisioning

To determine the rates at which helpers within their natal groups (i.e., all subordinate, and therefore non-breeding, group members still residing within the group in which they born) cooperatively provision the nestlings of the dominant pair, provisioning behaviour was recorded for all breeding attempts throughout the study period in which the nestlings survived to the standard recording days. A video camera was placed on a low tripod below the nest to record the birds entering the nest on the mornings of the 6th to 12th days (inclusive) after the first egg in the focal clutch hatched (days that cover the period of highest nestling demand; the effects of variation in brood age were then controlled in our analysis; see below). At least 5 days before video recording started, we caught every bird in the group apart from the dominant female to confirm group composition and mark each bird's vent feathers with a unique black dye mark to facilitate their identification on provisioning videos. On recording days, video cameras were set up at a standardized time following sunrise to record provisioning for approximately 3 hours per nest per day (yielding a total of 289 days of recording over the 177 monitored broods in groups with one or more helpers within their natal group; median of 2, range 1 - 6, days per brood). Within-nest cameras have confirmed that all nest visits in which the birds are not conspicuously carrying grass (events that were readily excluded from our provisioning rate calculations below), entail the visiting bird carrying a single food item to the nest and delivering it to the chicks (51). The videos were subsequently transcribed to determine the timing of each provisioning visit, the duration of the visit (from the bird entering the nest to exiting), and the identity of the provisioning bird (using its unique vent mark and information from its leg rings and bill colouration; which differs between the sexes). Whenever the bill of the provisioning bird was visible on their approach to the nest, we also categorised the size of the food item being delivered; simply 'large' if it was evidently longer than the bird's bill or 'short' if it was not.

We used the resulting provisioning data set to calculate the number of provisioning visits that each group member made during each observation period (termed 'provisioning number' within our methods; our analyses of provisioning rate entailed fitting provisioning number as the response term while accounting for

the effects of variation in the overall duration of the observation period using an offset; see below). In some cases, we were unable to reliably identify all group members, adding uncertainty to our provisioning number estimates. We therefore excluded any provisioning number estimates derived from observation periods in which there were five or more provisioning visits in which the feeder was of uncertain identity (72 rate estimates excluded). To address the residual uncertain in the provisioning number estimates derived from the observation periods containing one to four feeds by birds of uncertain identity, we set each bird's provisioning number estimate for these observation periods to be the integer midway between the lowest and highest possible provisioning number for that bird in that period given any partial identity information that was available for the feeders of uncertain identity. This yielded a final dataset containing 1,338 daily provisioning number measures for subordinates (helpers) of known sex within their natal groups for whom age was known with less than 180 days of uncertainty.

Quantifying the prospecting behaviour of natal subordinates

Automated radio-tracking using Encounternet

We used Encounternet (31, 32) to identify extra-territorial prospecting movements by natal subordinate sparrow weavers. This system is a wireless sensor network formed by an array of stationary radio receivers (termed 'base stations') that log the radio-signals of any animal-mounted transmitters (termed 'tags'; used here in transmit-only mode) within range. The logs collated by the base stations provide information on the tag (and therefore animal) ID detected, the date and time of detection and the signal strength (expressed as Received Signal Strength Indicator [RSSI] values). Between February and April 2017, we fitted Encounternet tags to 32 adult subordinate birds, using a figure-of-eight leg harness made of a stretchable, porous material that was stuck to the tag. The total mass of the tag and harness was ~1.2g (2.6-3.1% of the body mass of the tagged birds at fitting; Figure 3a). Field observations after tag fitting confirmed that none of the tagged birds showed any signs of affected behaviour or impaired movement, and our results suggest that they still regularly engaged in extra-territorial movements. All tags were retrieved from the birds before the end of April 2017, when the wet (breeding) season ends in the study site. Tag signal strength seemed to stay relatively constant during the period of data collection. The tagged birds were all (non-breeding) subordinates that were resident on their natal territory (hereafter, their 'home' territory) at the time of tagging and remained so for the duration of the Encounternet deployment. All tags were set to transmit ID-coded pulses every five seconds. To track the locations of the tags across our study site, we set up an array of 35 Encounternet base station receivers, each placed in the central tree (typically the main roost tree) of 35 contiguous sparrow weaver territories (Figure S1). To ensure that the times at which tags were logged at different base stations

could be compared over short timescales (to infer tag movements), we regularly checked that the clocks of all base stations were synchronised (yielding a typical deviation of between 0 and 1 seconds; maximum 6 seconds). Base station batteries were changed every 10 days, before they were discharged.

To account for variation among base stations in detection sensitivity, we calibrated all units before deployment (32, 52). To calibrate the base stations, we attached two (transmitter) tags to a wooden pole with one of the tags' antenna positioned parallel to, and the other positioned perpendicular to, the focal base station's antenna (to account for different antenna angles when the tags were on free-flying birds (52). We then held the tags (on the pole) at a fixed distance of two meters from each base station and at a height of 1.70 meters for two minutes, resulting in 48 logged pulses with RSSI values for each base station. We then calculated the mean RSSI value logged by each base station ($mean_{Basestation}$) and the mean RSSI value over all base stations ($mean_{RSSI}$). For the 10 base stations for which $mean_{Basestation}$ was outside the range of $mean_{RSSI} \pm 1$ standard deviation (SD), we adjusted the signal strength (RSSI) value of all logs from these base stations during analysis by adding $mean_{RSSI}$-$mean_{Basestation}$ (to avoid an over or underestimation of the distance between tagged birds and the focal base stations). In order to infer from the RSSI values when a tag was relatively close to a base station, we created a custom RSSI-distance calibration curve on the study site (Figure S4a), and then determined the estimated mean signal strength for a tag at 50 m (obtaining an RSSI value of -11.48). We subsequently used this estimated signal strength at 50 m as part of the decision pipeline for identifying our 'best estimate' locations for the tags (see below). During the RSSI-distance curve calibration, tags were on average detected 89% of the time when within 20 meters and 76% of the time when within 50 meters of a receiver (Figure 4b). We did not formally calibrate the individual tags (as well as the base stations), but we did verify qualitatively that all tags were yielding broadly comparable signal strengths at a fixed distance from a given base station prior to deployment.

Encounternet data processing

We processed the Encounternet logs for each tag separately, working through the continuous time series of logs for each tag (from across the base station network) to infer the locations of the tagged bird throughout the tag's deployment. We discarded all logs of a given tag from (i) the day on which the tag was deployed and the following day (53) (to allow time for the tagged bird to get used to the tag and recover from any capture-related disturbance), and (ii) a short period following any attempt to catch a member of the tagged bird's home group (from the time of the capture attempt to the end of the following day; given the potential for capture attempts to impact the birds' movements). A given tag's logs were then processed in moving

windows of 15 seconds and in time steps of 5 seconds. For each of these 15-second windows, we attempted to assign the tagged bird a 'best estimate' location following conservative set of rules (depicted as a flow diagram in Figure S5 and explained in the figure legend). Five birds were assigned to known locations (i.e. locations other than 'unknown') for a low proportion of their total tracked time (<30%), most likely due to tag failure, and so were excluded from further analyses. The average proportion of time that the remaining 27 tagged birds were assigned known locations was 73%. Note that with the rule set for location assignment (Figure S5), a tag having weak transmission strength (e.g., due to tag error or signal obstruction) would not cause it to be falsely assigned 'non-home' locations (that might later be interpreted as prospecting), because assignment to 'non-home' locations required that the tag was logged with a stronger signal strength at a non-home group than the home group (Figure S5).

We then processed the resulting time series of 'best estimate' locations for the tagged bird (one every 5 seconds) to identify extra-territorial prospecting forays using a conservative approach that should minimise the chance of false positives. Consecutive 15 second windows assigned to the same location were combined to represent 'time periods' for which our best estimate location was on a given territory ('unknown' locations were removed from the tag's location time series prior to this step, as they could occur while the bird was at any location; see above). Using this dataset, we identified prospecting forays as events that satisfied *all* of the following criteria: (i) a single 'time period' or set of contiguous time periods for which the tagged bird had been assigned known locations that were not the tagged bird's 'home' territory for 15 seconds (ii) during this contiguous non-home time period, the tagged bird's best-estimate locations were known locations for >15 seconds and (iii) the furthest assigned location during this contiguous non-home time period was >250 metres from their home territory's base station (approximately the centre of their home territory). As the centres of neighbouring groups' territories within our study site are always within 250 m of each other (Figure S1), this approach should ensure that movements of birds to the boundary of their home territory (e.g., during territorial boundary disputes with neighbours (25)) were not misclassified as extra-territorial prospecting forays. Thus the 'forays' characterised by these criteria are likely to constitute movements *beyond* the territories of neighbouring groups. This conservative approach will leave our analyses underestimating the true incidence of more local forays, by excluding true forays to neighbouring groups. However, shared territory boundaries and regular inter-group interactions on them (25) should already provide the members of neighbouring groups with information on each other without the need to conduct such short-range forays. For each foray, we estimated 'foray duration' as the time elapsed between the focal bird's first 'best estimate' location outside their home territory and their subsequent first 'best

estimate' location back on their home territory. We estimated 'foray distance' as the linear distance between the bird's home territory base station (approximately the centre of their home territory) and the furthest 'best estimate' location that they were assigned during the foray. These 'foray distances' could therefore markedly underestimate the true distance travelled during the foray, because (i) the bird could have travelled on a complex path to and from the outer point on the foray, taking in many groups, and (ii) the furthest 'best estimate' location could be much closer to home than the true furthest location visited by the bird during the foray, as the former is constrained to be the location of a base station within our array. If birds travelled far beyond the boundary of our base station array, we would still typically expect to detect such forays, as while distant birds might have long periods of 'unknown' locations while far from the array, we would generally expect to log them passing through known 'non-home' locations within the array soon after leaving their home group and just before returning to it (a scenario that would also render 'foray duration' broadly accurate). This might not be the case, however, if the tagged bird's home group lay on the periphery of the base station array and the bird prospected directly out of the study area; a scenario in which the prospecting foray would not have been detected at all.

General statistical approach

Statistical models were fitted with a set of fixed effect predictors and a specific set of interactions between them that were considered *a priori* to be biologically plausible. We specify the fixed effects, interactions and (where appropriate) random effects fitted in each of our statistical models within the relevant sections below. We employed a full model approach, evaluating the statistical importance of each predictor using likelihood-ratio tests (LRT) to assess the significance of the change the explanatory power of the full model on removal of the focal predictor. If not statistically significant, interactive terms were removed from initially-specified full model to ease the interpretation of the effects of non-interactive terms. All non-interactive fixed effect predictors were retained within the full model regardless of their significance. We provide tables of results for all full models with the supplementary materials including model estimates, standard errors ('SE'), 95% confidence intervals (95% CI), and likelihood-ratio test results (χ^2 value, degrees of freedom of the test and p-value) for each fixed effect predictor. All statistical analyses were carried out using R 4.3.1. (54). Unless otherwise stated, statistical models were fitted using the R package 'lme4' (v1.1.29; (55)). Over-dispersion and zero-inflation of GdLMMs were checked by simulating scaled model residuals in the R package 'DHARMa' (v0.4.6; (56).

1. Modelling the age-specific dispersal probabilities of natal subordinates

We investigated whether sparrow-weaver subordinates within their natal groups exhibit a sex difference in the age-specific probability of dispersal from their natal group, by fitting a binomial generalised linear mixed model (GdLMM) to data reflecting whether or not they dispersed within a given year-long age window of their lives as a natal subordinate. A sex difference in age-specific dispersal from the natal group is of particular interest as it will drive sex differences in both (i) the time spent within the natal group (relevant to the accrual of downstream direct fitness benefits from helping, as envisaged in the Philopatry hypothesis) and (ii) the need to prospect for dispersal opportunities (relevant to the Dispersal trade-off hypothesis). All individuals hatched into our population between September 2007 and April 2014 that reached six months of age contributed to our analysis (individuals under six months of age very rarely disperse) and we utilised group census data up until April 2016 to determine if and when they dispersed (giving all individuals a minimum of 2 years of monitoring in which to disperse). The lives of each of the focal individuals were divided into year-long 'age windows' from birth onwards. Each year-long age window that the individual started as a subordinate within its natal group (and before April 2016) contributed a line of data to the data set, and was flagged to reflect whether they were (1) or were not (0) observed to have dispersed away from their natal group to another study group within our population during that year of life. Our analysis therefore focussed on known dispersal events. A small number of unringed adults born outside our study population do enter our study groups each year, suggesting that a small number of adults born within our study population probably also disperse beyond its boundaries each year (23); unobserved dispersal events that this analysis will therefore miss. As males disperse significantly further than females in this population (23), and accordingly males are also more likely than females to enter our study population from outside (23), it would seem that males are more likely to be making undetected dispersals beyond the boundaries of our study site than females are. The key finding from this analysis, that males show a higher age-specific probabilities of dispersal than females is therefore if anything likely to underestimate the true magnitude of this sex differences in dispersal probability. This approach resulted in a data set of 812 year-long windows for 338 individuals (178 males and 160 females) monitored as natal subordinates within 36 social groups. The full model contained the following fixed effect predictors: the subordinate's sex, age class during the focal year-long age window (as a 4-level categorical variable: <1 year old; 1-2 years old, 2-3 years old, and > 3 years old; this last age class therefore captured any year-long age windows in which the focal individual was 3 years or older at the start of the age window), and the interaction between its sex and age class. Breeding season of hatching, individual ID and natal group ID were included as random effect intercepts.

2. Modelling the cooperative provisioning traits of natal subordinates

To investigate whether there is a sex difference in the nestling provisioning (helping) rates of natal subordinates, we fitted a zero-inflated negative binomial GdLMM using the R package 'glmmTMB' (v1.1.7; (57)). We modelled provisioning rate (feeds / hour) by fitting the birds' 'provisioning number' measure as the response term (the number of provisioning visits it conducted during a given ~3 hour observation period; see above), with the duration of the observation period fitted as an offset. We included the following fixed effect predictors in the full model: the sex of the bird, their age (a 4-level factor: < 1 year, 1 year – 2 years, 2 years – 3 years, and > 3 years), the interaction between sex and age (given the possibility that the magnitude of sex differences changes with age), brood size (as a continuous variable, 1 to 3 nestlings) and brood age (a 7-level factor, 6 to 12-day old, given the potential for non-linear effects). Breeding year, social group ID, clutch ID and individual ID were included as random intercepts. The model was fitted to 1,338 observations of provisioning number by 314 different natal subordinates feeding 177 broods in 38 social groups. We found evidence for zero-inflation (zero-inflation parameter ± SE = -1.605 ± 0.181) and over-dispersion (dispersion parameter = 2.87), which were accounted for by our zero-inflated negative binomial model. To investigate whether there is a sex difference in natal subordinate provisioning visit durations (time spent within the nest chamber, from entry to exit, during which the provisioning bird interacts with the brood), we fitted a linear mixed model to the provisioning visit durations of the 5,034 provisioning events that natal subordinates conducted during the observation periods monitored above. The full model included the same fixed and random effect predictors as the analysis of provisioning rate described above. Provisioning visit duration was 'log+1' transformed to fulfil the assumption of normality in model residuals. To investigate whether there is a sex difference in the size of the food items that natal subordinates provisioning to broods, we fitted a binomial GdLMM to the binomial prey item size information (large or small) collected from the 1,325 provisioning events in which the focal bird's bill was visible prior to entering the nest (see above). We analysed the probability that the prey item was large, with a full model that included the same fixed and random effect predictors as the analysis of provisioning rates described above.

3. Modelling the probability of acquiring dominance within the natal group

We investigated sex differences in the probability that natal subordinates inherit a dominant (breeding) position within their natal group using binomial GdLMMs, As the probability of inheriting natal dominance (and any sex difference therein) may change with a natal subordinate's age, we conducted different models each focussing on the dominance inheritance prospects of subordinates of a given age: one model at 0.5 years of age, one at 1 year of age, one at 2 years of age and one at 3 years of age. The data set for each model comprised all birds that were known to be subordinate within their natal group at the focal age, and

modelled whether or not they ultimately became dominant within their natal group. Subordinates were only included in the analysis if dominance turnovers were monitored within their natal group for a minimum of 2 years after the date on which the subordinate reached the focal age. Sex was included as a fixed effect predictor in these models. Breeding season of hatching and natal group ID were included as random intercepts. We also verified that similar patterns were reflected in a simple contingency table test for a sex difference in the proportion of all dominance acquisition events for a given sex in which the winner took dominance within their natal group. As subordinates could also conceivably gain a downstream direct fitness benefit from natal helping if they take a dominance position via 'territorial budding' from the natal territory (i.e., founding a new group on territory previously held by their natal group (1)), we then repeated our modelling analysis above including within the 'natal dominance inheritance events' events in which the focal bird did not inherit dominance within the natal *group* but instead became dominant by founding a new group via probable 'territorial budding'. Such 'budding' events typically occurred towards the edge of the natal group's territory, leaving it possible that they constitute 'budding' into regions whose historical defence by the natal group could have been facilitated by the natal subordinate's past contributions to natal helping (the mechanism relevant to the Philopatry hypothesis (1)). Using the 88 dispersal events in the dataset, we used binomial GdLMMs to explain the probability of dispersing into subordinate or dominant positions, including sex as a fixed effect predictor, and breeding season of hatching and natal group ID as random intercepts.

4. Modelling the prospecting behaviour of natal subordinates

To investigate whether there is a sex difference in the daily rate of extra-territorial prospecting (number of forays per day) we employed a Poisson GdLMM. To investigate whether there is a sex difference in mean 'foray duration' and mean 'foray distance' (see above) we employed LMMs. In each of these three models, we included the same set of fixed effect predictors: age of the individual (as a continuous variable), sex, provisioning status of their home group (2-level factor [yes/no] to capture whether their home group as provisioning nestlings at the time), and the interaction between sex and provisioning status. In all three models we included bird ID and home territory ID as random intercepts. In the model of the daily rate of prospecting, we also included observation ID as a random intercept, to account for overdispersion (58). All three models used data from the 27 individuals with working tags (see above; 13 males and 14 females).

To investigate the existence of a trade-off between cooperative nestling provisioning and prospecting, we tested whether these traits were correlated at the individual level. For this analysis, we used the Encounternet data from the 13 tagged subordinates (6 males and 7 females) whose prospecting rates were

quantified during a nestling feeding period within their group. For these birds we therefore had daily estimates of their prospecting rate, as well as estimates of their nestling provisioning rate from those mornings in which provisioning observations were also conducted (see above). To estimate a proxy for each bird's general level of prospecting effort, we calculated the bird's prospecting rate over a given number of days preceding each day of provisioning observations (see below). The full model included this proxy for the focal bird's prospecting effort as the main fixed effect predictor of interest in a Poisson GdLMM of daily provisioning feeds of these birds, including duration of the provisioning behaviour observation as an offset (i.e., effectively modelling provisioning rate via a Poisson model). We also included subordinate sex, brood age (as a continuous predictor in this case due to lower sample size), brood size and the interaction between prospecting rate and subordinate sex as fixed effects. Group ID and bird ID were included as random effect intercepts. The sample size for the analysis was 43 daily measures of provisioning rate for the 13 tagged subordinates. In the main text, we show results when prospecting rates were calculated over a window of three days prior to the focal daily measure of provisioning rate, but we confirmed through sensitivity analyses that the observed negative association between the two traits was evident over a range of time window lengths (Figure S3).

Acknowledgments

We would like to thank the many team members who contributed to the collection of the long-term data over the years, Northern Cape Conservation for permission to carry out the research, Nigel Bennett for invaluable assistance with in-country permissions, and E. Oppenheimer & Son, the Tswalu Foundation, and all at Tswalu Kalahari Reserve for their support in the field and the collection and sharing of the reserve-wide rainfall data. We also thank Ben Hatchwell and Erik Postma for insightful discussions. The long-term field study was funded principally by a BBSRC David Phillips Research Fellowship and a NERC Blue Skies Research Fellowship to A.J.Y. (BB/H022716/1 and NE/E013481/1) and P.C.-L. was supported by a BBSRC-funded PhD studentship (BB/M009122/1). A BBSRC David Phillips Research Fellowship to C.R. (BB/G023913/1 and BB/G023913/2) funded the Encounternet equipment that was used in this study. NB was supported by an ALW-NWO open competition grant (ALWOP 824.15.012) to MN.

References

1. G. E. Woolfenden, J. W. Fitzpatrick, The Inheritance of Territory in Group-Breeding Birds. *Bioscience* **28**, 104–108 (1978).
2. A. Cockburn, Evolution of helping behavior in cooperatively breeding birds. *Annu Rev Ecol Syst* **29**, 141–177 (1998).
3. T. H. Clutton-Brock, *et al.*, Evolution and development of sex differences in cooperative behavior in meerkats. *Science* **297**, 253–256 (2002).
4. D. A. Williams, A. M. Hale, Female-biased helping in a cooperatively breeding bird: Female benefits or male costs? *Ethology* **113**, 534–542 (2007).
5. P. A. Downing, A. S. Griffin, C. K. Cornwallis, Sex differences in helping effort reveal the effect of future reproduction on cooperative behaviour in birds. *Proceedings of the Royal Society B* **285**, 20181164 (2018).
6. P. Fenner, T. E. Currie, A. J. Young, Sex differences in dispersal predict sex differences in cooperation in cooperatively breeding birds and mammals. *bioRxiv* (2023).
7. D. Canestrari, J. M. Marcos, V. Baglione, Effect of parentage and relatedness on the individual contribution to cooperative chick care in carrion crows Corvus corone corone. *Behav Ecol Sociobiol* **57**, 422–428 (2005).
8. M. Zöttl, *et al.*, Differences in cooperative behavior among Damaraland mole rats are consequences of an age-related polyethism. *Proc Natl Acad Sci* **113**, 10382–10387 (2016).
9. A. J. Young, A. A. Carlson, T. Clutton-Brock, Trade-offs between extraterritorial prospecting and helping in a cooperative mammal. *Anim Behav* **70**, 829–837 (2005).
10. S. A. Kingma, Direct benefits explain interspecific variation in helping behaviour among cooperatively breeding birds. *Nat Commun* **8**, 1094 (2017).
11. E. D. Doerr, V. A. J. Doerr, Dispersal range analysis: Quantifying individual variation in dispersal behaviour. *Oecologia* **142**, 1–10 (2005).
12. A. J. Young, G. Spong, T. H. Clutton-Brock, Subordinate male meerkats prospect for extra-group paternity: alternative reproductive tactics in a cooperative mammal. *Proceedings of the Royal Society of London B* **274**, 1603–1609 (2007).
13. S. A. Kingma, J. Komdeur, M. Hammers, D. S. Richardson, The cost of prospecting for dispersal opportunities in a social bird. *Biol Lett* **12**, 20160316 (2016).
14. S. A. Kingma, K. Bebbington, M. Hammers, D. S. Richardson, J. Komdeur, Delayed dispersal and the costs and benefits of different routes to independent breeding in a cooperatively breeding bird. *Evolution* **70**, 2595–2610 (2016).
15. A. R. Ridley, N. J. Raihani, M. J. Nelson-Flower, The cost of being alone: The fate of floaters in a population of cooperatively breeding pied babblers Turdoides bicolor. *J Avian Biol* **39**, 389–392 (2008).
16. A. J. Young, S. L. Monfort, Stress and the costs of extra-territorial movement in a social carnivore. *Biol Lett* **5**, 439–41 (2009).
17. N. Maag, *et al.*, Dispersal Decreases Survival but Increases ReproductiveOpportunities for Subordinates in a Cooperative Breeder. *American Naturalist* **199**, 679–690 (2022).
18. D. L. Cram, J. D. Blount, A. J. Young, The oxidative costs of reproduction are group-size dependent in a wild cooperative breeder. *Proceedings of the Royal Society B* **282**, 20152031 (2015).
19. R. Heinsohn, S. Legge, The cost of helping. *Trends on Ecology and Evolution* **14**, 53–57 (1999).
20. N. E. Collias, E. C. Collias, Cooperative breeding behaviour in the white-browed sparrow weaver. *Auk* **95**, 472–484 (1978).
21. D. M. Lewis, Cooperative breeding in a population of white-browed sparrow weavers Plocepasser mahali. *Ibis* **124**, 511–522 (1982).
22. X. Harrison, J. E. York, D. L. Cram, M. C. Hares, A. J. Young, Complete reproductive skew within white-browed sparrow weaver groups despite outbreeding opportunities for subordinates of both sexes. *Behav Ecol Sociobiol* **67**, 1915–1929 (2013).
23. X. Harrison, J. E. York, A. J. Young, Population genetic structure and direct observations reveal sex-reversed patterns of dispersal in a cooperative bird. *Mol Ecol* **23**, 5740–5755 (2014).

24. P. J. Greenwood, Mating systems, philopatry and dispersal in birds and mammals. *Anim Behav* **28**, 1140–1162 (1980).
25. J. E. York, K. J. Wells, A. J. Young, Dominance-related contributions to collective territorial defence are adjusted according to the threat. *Anim Behav* **158**, 25–34 (2019).
26. D. M. Lewis, Dispersal in a population of white-browed sparrow weavers. *Condor* **84**, 306–312 (1982).
27. P. Capilla-Lasheras, X. Harrison, E. M. Wood, A. J. Wilson, A. J. Young, Altruistic bet hedging and the evolution of cooperation in a Kalahari bird. *Sci Adv* **7**, eabe8980 (2021).
28. L. Walker, *et al.*, Prolactin and the regulation of parental care and helping behavior in cooperatively breeding white-browed sparrow weaver societies. *bioRxiv* (2021).
29. O. O'Callaghan, Social effects on adult survival in a wild cooperative bird. *MSc Thesis. University of Exeter.* (2021).
30. E. Wood, Causes and fitness consequences of telomere dynamics in a wild social bird. *PhD Thesis. University of Exeter*. (2017).
31. C. Rutz, *et al.*, Automated mapping of social networks in wild birds. *Current Biology* **22**, R669–R671 (2012).
32. D. J. Mennill, *et al.*, A novel digital telemetry system for tracking wild animals: A field test for studying mate choice in a lekking tropical bird. *Methods Ecol Evol* **3**, 663–672 (2012).
33. G. Whitney, Genetic substrates for the initial evolution of human sociality. I. Sex chromosome mechanisms. *American Naturalist* **110**, 867–875 (1976).
34. E. L. Charnov, Kin selection and helpers at the nest: effects of paternity. *Anim Behav* **29**, 631–632 (1978).
35. X. Harrison, J. E. York, D. L. Cram, A. J. Young, Extra-group mating increases inbreeding risk in a cooperatively breeding bird. *Mol Ecol* **22**, 5700–5715 (2013).
36. W. D. Koenig, E. L. Walters, Age-related provisioning behaviour in the cooperatively breeding acorn woodpecker: Testing the skills and the pay-to-stay hypotheses. *Anim Behav* **82**, 437–444 (2011).
37. W. D. Koenig, R. L. Mumme, F. A. Pitelka, "Female roles in cooperatively breeding acorn woodpeckers" in *Social Behaviour of Female Vertebrates*, S. K. Wasser, Ed. (Academic Press, 1983), pp. 235–261.
38. M. A. Cant, J. Field, Helping effort and future fitness in cooperative animal societies. *Proceedings of the Royal Society B* **268**, 1959–1964 (2001).
39. P. Capilla-lasheras, A. J. Wilson, A. J. Young, Mothers front-load their investment to the egg stage when helped in a wild cooperative bird. *bioRxiv*, 1–31 (2021).
40. A. F. Russell, N. E. Langmore, A. Cockburn, L. B. Astheimer, R. M. Kilner, Reduced egg investment can conceal helper effects in cooperatively breeding birds. *Science* **317**, 941–944 (2007).
41. A. J. Gaston, The evolution of group territorial behaviour and cooperative breeding. *Am Nat* **112**, 1091–1100 (1978).
42. M. F. Clarke, The pattern of helping in the Bell miner (Manorina melanophrys). *Ethology* **80**, 292–306 (1989).
43. H.-U. Reyer, Breeder-Helper-Interactions in the Pied Kingfisher Reflect the Costs and Benefits of Cooperative Breeding. *Behaviour* **96**, 277–303 (1986).
44. M. Zöttl, D. Heg, N. Chervet, M. Taborsky, Kinship reduces alloparental care in cooperative cichlids where helpers pay-to-stay. *Nat Commun* **4**,1341 (2013).
45. M. Double, A. Cockburn, Pre-dawn infidelity: females control extra-pair mating in superb fairy-wrens. *Proceedings of the Royal Society B* **267**, 465–470 (2000).
46. A. Peters, Testosterone and the trade-off between mating and paternal effort in extrapair-mating superb fairy-wrens. *Anim Behav* **64**, 103–112 (2002).
47. A. J. Van Noordwijk, G. De Jong, "Acquisition and Allocation of Resources: Their Influence on Variation in Life History Tactics" (1986).
48. L. Benoit, *et al.*, Accelerating across the landscape: The energetic costs of natal dispersal in a large herbivore. *Journal of Animal Ecology* **89**, 173–185 (2020).
49. L. A. Walker, J. E. York, A. J. Young, Sexually selected sentinels? Evidence of a role for intrasexual competition in sentinel behavior. *Behavioral Ecology* **27**, 1461–1470 (2016).
50. S. Leitner, P. Mundy, C. Voigt, Morphometrics of White-browed Sparrow-Weavers Plocepasser mahali in south-western Zimbabwe. *Ostrich* **80**, 99–102 (2009).

51. L. Walker, The evolution and regulation of cooperation in the wild. *PhD Thesis. University of Exeter*. (2015).
52. C. Rutz, *et al.*, Calibrating animal-borne proximity loggers. *Methods Ecol Evol* **6**, 656–667 (2015).
53. J. J. H. St Clair, *et al.*, Experimental resource pulses influence social-network dynamics and the potential for information flow in tool-using crows. *Nat Commun* **6**, 7197 (2015).
54. R Core Team, R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria (2022).
55. D. Bates, M. Machler, B. Bolker, S. Walker, Fitting Linear Mixed-Effects Models Using lme4. *J Stat Softw* **67**, 1–48 (2015).
56. F. Hartig, DHARMa: Residual diagnostics for hierarchical (multi-Level / mixed) regression models (2018).
57. M. E. Brooks, *et al.*, glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *R J* **9**, 378–400 (2017).
58. X. Harrison, Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ* **2**, e616 (2014).