Mothers front-load their investment to the egg stage when helped in a wild cooperative bird

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Data accessibility
The main datasets generated and analysed during the current study are available from the Dryad Digital Repository:
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Abstract

In many cooperative societies, including our own, helpers assist with the post-natal care of breeders' young, and may thereby benefit the *post-natal* development of offspring. Here we present evidence of a novel mechanism by which such post-natal helping could also have hitherto unexplored beneficial effects on *pre-natal* development: by lightening post-natal maternal workloads, helpers may allow mothers to increase their pre-natal investment per offspring. We present the findings of a decade-long study of cooperatively breeding white-browed sparrow weaver, *Plocepasser mahali,* societies. Within each social group, reproduction is monopolized by a dominant breeding pair, and non-breeding helpers assist with nestling feeding. Using a within-mother reaction norm approach to formally identify maternal plasticity, we demonstrate that when mothers have more female helpers they decrease their own *post-natal* investment per offspring (feed their nestlings at lower rates) but increase their *pre-natal* investment per offspring (lay larger eggs, which yield heavier hatchlings). That these plastic maternal responses are predicted by female helper number, and not male helper number, implicates the availability of post-natal helping *per se* as the likely driver (rather than correlated effects of group size), because female helpers feed nestlings at substantially higher rates than males. We term this novel maternal strategy "maternal front-loading" and hypothesize that the expected availability of *post-natal* help allows helped mothers to focus maternal investment on the *pre-natal* phase, to which helpers cannot contribute directly. Such cryptic maternally mediated helper effects on pre-natal development may markedly complicate attempts to identify and quantify the fitness consequences of helping.

Introduction

Maternal effects arising from variation in pre-natal maternal investment in the egg or fetus can have profound fitness consequences for mothers and offspring [1–3]. In social organisms, mothers are predicted to evolve investment strategies that maximize their fitness returns on investment according to their social environment [4–8]. Cooperatively breeding species are of particular interest in this regard, as helpers typically contribute to the post-natal feeding of the offspring of breeding females (hereafter 'mothers') and thus have the potential to impact the optimal level of maternal pre-natal investment *per offspring* [5,6,9,10]. Where mothers are assisted by variable numbers of helpers throughout their lives, selection may be expected to favor plastic strategies in which mothers adjust their pre-natal investment per offspring according to the likely availability of help during the post-natal period [6].

Different maternal strategies for adjusting pre-natal investment *per offspring* to the presence of helpers are hypothesized to evolve depending on how helpers impact the maternal payoff from pre-natal investment per offspring. The leading hypotheses (outlined below) focus on the mechanisms by which helpers could affect the optimal level of pre-natal investment per offspring, independent of variation in offspring number per breeding attempt (which could itself affect pre-natal investment per offspring via resource allocation trade-offs [11]). Empirical tests of these hypotheses therefore allow for the possibility that pre-natal investment per offspring is *also* affected by trade-offs with offspring number (e.g., clutch size in birds; which could itself be adjusted to helper number [12]).

Helpers have the potential to *decrease* the mother's optimal level of pre-natal investment per offspring, leading to strategies in which mothers *reduce* pre-natal investment per offspring when assisted by more helpers [5,6,13,14]. Such a maternal reduction in pre-natal investment per offspring when helped is typically referred to as a 'load-lightening' response ([5,12,15]; following the historical use of this term to describe helper-induced reductions in maternal investment per offspring at the post-natal stage [8,16]). The 'Load-Lightening Hypothesis' [5,8] for the adjustment of maternal *pre-natal* investment per offspring envisages that selection could favor such a maternal strategy if helpers (i) increase the overall provision of *post-natal* care per offspring (i.e., provide 'additive post-natal care'; [8]) and thereby (ii) compensate, in part or whole, for any maternal reduction in *pre-natal* investment per offspring when helped (formally modelled as the 'head start' scenario in [9]). Notably, this hypothesis requires that helper-derived post-natal care can compensate for reductions in maternal pre-natal investment (i.e., that investment can be 'substituted across stages'; [9]), which may not always be the case [9,17,18]. Indeed, there is ample evidence that pre-natal conditions, and pre-natal maternal investment in particular, can have formative effects on offspring phenotype and performance [2,3,17–21].

Helpers also have the potential to *increase* the mother's optimal level of pre-natal investment per offspring, leading to strategies in which mothers instead *increase* pre-natal investment per offspring when assisted by more helpers [6,9,10,22]. The 'Differential allocation hypothesis', for example, proposes that mothers should increase maternal investment under circumstances that increase their expected return on investment in their current breeding attempt, such as the presence of a high quality mate or more helpers [6,10,22–26]. This hypothesis was originally proposed in the context of non-cooperative species [23,24,26], before being verbally extrapolated to cooperative breeders, with the suggestion that, as helpers commonly increase the reproductive value of offspring by providing additive post-natal care, mothers should increase investment per offspring when helped [6,10,15,22,25,27]. More specifically, the provision of additive *post-natal* care by helpers may increase the mother's return on *pre-natal* investment per offspring wherever pre- and post-natal investment have positive interactive effects on offspring fitness (such that *post-natal* helping increases the effect of maternal *pre-natal* investment on offspring fitness; [9]). Indeed, mathematical models incorporating such interactive effects of pre- and post-natal investment per offspring (the 'silver spoon' scenario in [9]) predict that, where helpers contribute to post-natal care, mothers should *increase* both pre- and post-natal investment per offspring when helped.

Cooperatively breeding birds provide a fruitful testing ground for these hypotheses, given the ability to estimate maternal pre-natal investment per offspring across different helping contexts by measuring egg traits. Several studies of cooperative birds have now reported that, after controlling for variation in clutch size, mothers with (more) helpers lay smaller eggs; the pattern predicted by the load-lightening hypothesis (e.g., *Malurus cyaneus* [5]; *Corvus corone corone* [13]; *Vanellus chilensis* [28]; *Philetairus socius* [14]; see also [29] for an experimental demonstration in fish). Three studies of cooperative birds have reported no evident relationship between egg size and the availability of help [12,30,31], and just one study has reported the reverse relationship. Iberian magpie (*Cyanopica cooki)* mothers with more helpers lay larger eggs *and* feed their nestlings at higher rates, consistent with the predictions of the differential allocation hypothesis [9,22,25]. The situation may be more complex in some cases, however, as recent work suggests that the previously reported negative relationship between egg size and the availability of help in super fairy-wrens [5] becomes more positive under warmer conditions [10]. Given the overall weight of evidence for negative relationships across species, meta-analysis of these collated findings has led to the suggestion that helpers commonly *decrease* the mother's optimal level of pre-natal investment per offspring, and that the rationale of the load-lightening hypothesis may therefore commonly apply [15].

Crucially though, it has yet to be demonstrated that any of these associations between helper number and egg size in cooperative birds arise specifically from maternal *plasticity* (i.e., *within*-mother variation in egg size; see [29]). They could arise instead from among-mother variation in egg size being correlated with among-mother variation in helper number (e.g., mothers on higher quality territories might simply lay larger eggs and have more offspring that survive to become helpers). Indeed, a study that explicitly teased apart the effects of within- and among-mother variation in helper number found that the negative relationship initially detected between helper number and egg volume in red-winged fairy wrens (*Malurus elegans*) arose from among-mother variation in egg volume rather than maternal plasticity (i.e., within-mother variation; maternal plasticity was instead detected in clutch size), illustrating the importance of taking this approach [12]. While this same approach has revealed maternal plasticity in egg size according to abiotic conditions (e.g., temperature; [10]), evidence of maternal plasticity in egg size according to the availability of help *per se* does not yet exist for cooperative birds [12]. As such, it remains unclear whether avian mothers ever do adjust their pre-natal investment per offspring according to helper number, and whether any such maternal plasticity conforms to the predictions of the load-lightening or differential allocation hypotheses.

Here, we use a long-term field study of cooperatively breeding white-browed sparrow weavers, *Plocepasser mahali*, to test the key predictions of these load-lightening and differential allocation hypotheses for the evolution of maternal plasticity in pre-natal investment. We do so by testing for maternal plasticity in both pre-natal investment per offspring (egg volume; while accounting for effects of clutch size) and post-natal investment per offspring (maternal nestling provisioning rate) according to the availability of help. We test for plasticity using a maternal reaction norm approach, in which we isolate the effects of *within*-mother variation in helper number on maternal investment (i.e., maternal plasticity) from potentially confounding effects of variation among mothers [12,32]. White-browed sparrow-weavers live in social groups of 2-12 birds, in which a single dominant female ('the mother') and male monopolize within-group reproduction and non-breeding subordinate 'helpers' of both sexes help to feed their nestlings [33,34]. Helpers are typically past offspring of the dominant breeding pair, and hence are usually helping to rear close kin [33]. Female helpers feed nestlings at approximately twice the rate of male helpers, and accordingly female helper number has a demonstrably causal positive effect on the total rate at which broods are fed while male helper number does not (i.e., only female helpers provide demonstrably additive post-natal care; [35]). That only female helpers provide demonstrably additive post-natal care provides an unusual opportunity to distinguish the hypothesized pre-natal maternal responses to the availability of additive help (which should manifest in this species as maternal responses to the number of *female* helpers) from maternal responses to group size more generally (which could influence maternal investment through mechanisms other than helping; [36,37]).

Sparrow-weaver mothers lay small clutches of 1-3 eggs (modal clutch size = 2 eggs) and do not adjust their clutch size according to helper numbers (see Results). Indeed, given their small clutch size, subtle adjustments in pre-natal maternal investment may be more readily achieved through changes in investment per egg than through changes in clutch size. The focal hypotheses assume that laying mothers are able to predict the helper numbers that they will have during the post-natal rearing period, in order to adjust their own pre-natal investment per offspring accordingly. This should be straightforward in sparrow-weaver societies, as both male and female helper numbers at laying strongly predict male and female helper numbers respectively during the post-natal rearing period (Figure S1). We assess pre-natal maternal investment per offspring by quantifying egg volume, which in this species is strongly correlated with egg mass at laying and strongly predicts nestling mass at hatching (see Results). Maternal variation in egg volume is therefore likely to have fitness implications for offspring (and their mothers), not least because nestling mass at hatching positively predicts nestling survival to fledging in this species [35].

We test the following key predictions of the two focal hypotheses. The load-lightening hypothesis (‘head start’ scenario in [9]) predicts that sparrow-weaver mothers should decrease egg volume when assisted by more female, but not male, helpers. The differential allocation hypothesis (‘silver spoon’ scenario in [9]) predicts that sparrow-weaver mothers should increase both egg volume and their nestling provisioning rate when assisted by more female, but not male, helpers. To test these predictions, we first investigate whether within-mother variation in female and male helper numbers at laying predicts variation in egg volume (utilizing a large longitudinal data set; 490 eggs laid in 271 clutches by 62 mothers in 37 social groups; 1-21 eggs [median = 7] per mother). These analyses of egg volume control for any effects of variation in clutch size, and we confirm that our findings are not complicated by parallel maternal plasticity in clutch size according to helper numbers (by verifying that within-mother variation in female and male helper numbers does not predict clutch size). We then investigate whether within-mother variation in female and male helper numbers predict variation in the mother’s nestling feeding rate (again utilizing a large longitudinal data set; 124 broods being fed by 50 mothers in 34 social groups; 1-7 broods [median = 2] per mother). Our analyses also allow for effects of variation in abiotic conditions (rainfall and temperature) on mean levels of maternal investment [38,39].

Results

The patterns and implications of maternal variation in egg volume

Sparrow-weavers show appreciable variation in egg volume both within and among mothers (Figure 1a). The average egg volume per mother was 3.665 cm^3 (range = 2.850 cm^3 to 4.462 cm^3); with a maternal repeatability for egg volume of 69.3% (i.e., the amount of total variation in egg volume explained by a mother ID random effect; $\chi^2_1 = 129.89$, $p < 0.001$). Egg volume appears to provide a valid proxy for pre-natal maternal investment per offspring, as higher volume eggs were heavier at laying (Figure 1b; $\chi^2_1 = 625.98$, $p < 0.001$) and yielded heavier nestlings at hatching (Figure 1c; $\chi^2_1 = 27.23$, $p < 0.001$). These relationships also hold within mothers, illustrating that maternal *plasticity* in egg volume is also a key source of variation in both egg mass at laying (effect of *within*-mother variation in egg volume on egg mass ± SE = 0.949 ± 0.032 g / cm^3; N = 391 eggs from 59 mothers; $\chi^2_1 = 461.66$, $p < 0.001$) and nestling mass at hatching (effect of *within*-mother variation in egg volume on hatchling mass ± SE = 0.846 ± 0.228 g / cm^3; N = 193 eggs from 54 mothers; $\chi^2_1 = 13.22$, $p < 0.001$). Laying larger eggs could therefore have fitness consequences for mothers and the resulting offspring, as larger eggs yield heavier hatchlings (Figure 1c) and heavier hatchlings in this species are more likely to survive to fledging [Table S3 in 35].

Maternal plasticity in pre-natal investment per offspring: individual mothers lay larger eggs when they have more female helpers

Modelling the causes of variation in egg volume revealed that mothers with more female helpers at laying laid significantly larger eggs (Figure 2a; Table 1; $\chi^2_1 = 4.31$, $p = 0.038$). To identify whether this population-level relationship arose in part from a maternal plastic response to female helper numbers, we repeated the analysis after partitioning variation in female (and male) helper numbers into their *within*-mother ('Δ female helper number') and *among*-mother ('μ female helper number') components. This analysis revealed evidence of maternal plasticity in egg volume according to female helper numbers (i.e., a maternal reaction norm to variation in female helper number): *within*-mother variation in female helper number significantly positively predicted egg volume (Figure 2b; Table 2; Δ female helper number effect; $\chi^2_1 = 4.36$, $p = 0.037$). Among-mother variation in female helper number did not significantly predict egg volume (Table 2; μ female helper number; $\chi^2_1 = 0.10$, $p = 0.755$). A significant difference between the effect sizes for the within- and among-mother components of female helper number would indicate that consistent differences in egg volume among mothers (other than those arising from the maternal plastic response to female helper number) also contribute significantly to the population-level relationship between female helper number and egg volume detected in Table 1. Our analyses reveal no such evidence; the effect size estimates for the within- and among-mother components of female helper number in Table 2 do not differ significantly (difference between the 'among' and 'within' slopes ± SE = -0.010 ± 0.029 cm^3 / female helper; $\chi^2_1 = 0.13$, $p = 0.718$).

Male helper number did not significantly predict variation in egg volume, either in our initial analysis at the population level (Table 1; $\chi^2_1 = 0.61$, $p = 0.435$) or following the partitioning of the helper number terms into their within- and among-mother components (Table 2; Δ male helper number effect; $\chi^2_1 = 0.57$, $p = 0.450$; μ male helper number effect; $\chi^2_1 = 0.09$, $p = 0.769$; the effect size estimates for these terms did not significantly differ; $\chi^2_1 = 0.001$, $p = 0.982$). The point estimate for the effect size of the maternal plastic response in egg volume to female helper number (Δ female helper number effect ± SE = 0.019 ± 0.009 cm^3 / female helper; Table 2) was also approximately twice that for male helper number

(Δ male helper number effect ± SE = 0.008 ± 0.010 cm^3 / male helper; Table 2), though these effect sizes do not significantly differ ($\chi^2_1 = 0.52$, $p = 0.471$). Egg volume was also predicted by the position of the egg in the laying order (the first laid egg was larger; Table 1; $\chi^2_1 = 23.20$, $p < 0.001$) and by environmental temperature and rainfall (Table 1; the effects of these abiotic predictors are discussed in detail in Supplementary materials A). We found no evidence that the magnitude of the helper number effects on egg volume depended on clutch size or egg position for either female or male helper numbers (for all interactions $\chi^2_1 < 0.26$, $p > 0.593$).

Our analyses also allowed for an effect of clutch size on egg volume, but no such association was detected (Table 1, $\chi^2_1 = 0.01$, $p = 0.918$). Separate analyses also revealed no evidence that mothers adjust their clutch size according to helper numbers. Analysis at the population level revealed that clutch size was not significantly predicted by either the number of female helpers at laying (effect size ± SE = -0.046 ± 0.041 eggs / female helper, $\chi^2_1 = 1.29$, $p = 0.256$; N = 344 clutches laid by 66 mothers in 37 social groups; 1-15 clutches [median 4] per mother) or the number of male helpers at laying (effect size ± SE = -0.043 ± 0.047 eggs / male helper, $\chi^2_1 = 0.85$, $p = 0.357$). We found similar results after partitioning variation in helper numbers; clutch size was not significantly predicted by within- or among-mother variation in female helper number (Δ female helper number effect ± SE = -0.047 ± 0.051 eggs / female helper; $\chi^2_1 = 0.85$, $p = 0.358$; µ female helper number effect ± SE = -0.043 ± 0.065 eggs / female helper; $\chi^2_1 = 0.43$, $p = 0.510$) or male helper number (Δ male helper number effect ± SE = -0.049 ± 0.060 eggs / male helper; $\chi^2_1 = 0.66$, $p = 0.416$; µ male helper number effect ± SE = -0.033 ± 0.073 eggs / male helper; $\chi^2_1 = 0.21$, $p = 0.650$). The order of the clutch within the breeding season (e.g., a mother's first, second or third clutch) did not explain variation in clutch size either ($\chi^2_1 = 0.50$, $p = 0.478$).

Maternal plasticity in post-natal investment: individual mothers provision nestlings at lower rates when they have more female helpers

Mothers that had more female helpers during the nestling period provisioned their nestlings at significant lower rates (Figure 2c; Table 3; $\chi^2_1 = 5.39$, $p = 0.020$). Partitioning the female helper number predictor into its within- and among-mother components revealed evidence of maternal plasticity in nestling provisioning rate according to female helper numbers (i.e., a maternal reaction norm to variation in female helper number): *within*-mother variation in female helper number significantly negatively predicted a mother's provisioning rate (Figure 2d; Table 4; Δ female helper number effect; $\chi^2_1 = 4.24$, $p = 0.040$). Among-mother variation in female helper number did not significantly predict a mother's provisioning rate (Table 4; μ female helper number; $\chi^2_1 = 1.14$, $p = 0.285$). A significant difference between the effect sizes for the within- and among-mother components of female helper number would indicate that consistent differences in provisioning rate among mothers (other than those arising from the maternal plastic response to female helper number) also contribute significantly to the population-level relationship between female helper number and maternal provisioning rate detected in Table 3. Our analyses reveal no such evidence; the effect size estimates for the within- and among-mother components of female helper number in Table 4 do not differ significantly (difference between the 'among' and 'within' slopes ± SE = 0.233 ± 0.419 feeds / hour / female helper; $\chi^2_1 = 0.31$, $p = 0.578$).

Male helper number did not significantly predict variation in maternal provisioning rate, either in our initial analysis at the population level (Table 3; $\chi^2_1 = 0.10$, $p = 0.754$) or following the partitioning of the helper number terms into their within- and among-mother components (Table 4; Δ male helper number effect; $\chi^2_1 = <0.01$, $p = 0.986$). The point estimate for the effect size of the maternal plastic response in provisioning rate to female helper number (Δ female helper number effect ± SE = -0.56 ± 0.27 feeds / hour / female helper; Table 4) was also larger than that for male helper number (Δ male helper number effect ± SE = 0.01 ± 0.31 feeds / hour / female helper; Table 4), though these effect sizes do not significantly differ ($\chi^2_1 = 1.57$, $p = 0.210$). Maternal nestling provisioning rates were also significantly positively related to brood size (Table 3; $\chi^2_1 = 30.02$, $p < 0.001$) and were predicted by environmental temperature and rainfall (Table 3; discussed in detail in Supplementary materials A). We found no evidence that the magnitude of the helper number effects on maternal provisioning rate depended on brood size for either female or male helper numbers (for all interactions $\chi^2_1 < 2.10$, $p > 0.148$).

Discussion

To test the predictions of the 'load-lightening' and 'differential allocation' hypotheses for the evolution of pre-natal investment strategies in cooperative breeders, we investigated the patterns of maternal plasticity in both pre- and post-natal investment per offspring in white-browed sparrow weaver societies. Using a within-mother reaction norm approach, our analyses revealed the first formal evidence of maternal plasticity in egg investment according to the availability of help in a cooperatively breeding bird (see Introduction and [29]). When sparrow-weaver mothers had more female helpers they laid modestly but significantly larger eggs (and larger eggs yield heavier hatchlings, which are more likely to survive to fledging; [see Table S3 in 35]). This maternal plastic response runs counter to the leading 'load-lightening hypothesis' (which predicts that helped mothers should lay smaller eggs; [5,9]) and counter to general expectation given empirical work to date [15]. The 'differential allocation hypothesis' does predict that helped mothers should lay larger eggs (as we observe), but is thought to predict that helped mothers should also feed their nestlings at higher rates (i.e., mothers should increase both pre- *and* post-natal investment per offspring when helped; see 'silver spoon' scenario in [9]). By contrast, our findings reveal a novel maternal strategy in which mothers with more (female) helpers appear to *increase* pre-natal investment per offspring (lay larger eggs) but *decrease* post-natal investment per offspring (feed their nestlings at lower rates). We term this strategy 'maternal front-loading', as mothers effectively front-load their investment to the pre-natal stage when helped. We consider adaptive explanations for this strategy below, along with its implications for identifying the benefits of helping in cooperative societies. Maternal front-loading provides a mechanism by which *post-natal* helping could have beneficial effects on the *pre-natal* development of young.

While relationships between helper number and egg size have previously been reported in cooperatively breeding birds ([15]; and see Introduction), our findings evidence that such a pattern can arise from within-mother plasticity. This is important as recent work has highlighted that population-level relationships between helper number and egg size (i.e., those reported to date: e.g., [5,10,13,14,22]) can arise from among-mother variation in egg size rather than within-mother plasticity [12]. Furthermore, that sparrow-weaver mothers appear to significantly adjust egg size according to female helper number and not male helper number implicates the availability of post-natal helping *per se* as the likely driver of this plastic maternal response, rather than correlated variation in group size (as female helpers feed nestlings at twice the rate of male helpers, and only female helper number has a demonstrably causal positive effect on the overall rate of nestling provisioning; [35]). Indeed, as female and male helper numbers at laying strongly predict helper numbers during the post-natal care period (Figure S1), sparrow-weaver mothers should have sufficient information at laying to adjust their egg volume to the future availability of post-natal help, were it adaptive to do so. Such a pattern of investment per egg could conceivably emerge as a by-product of a helper effect on the mother's optimal clutch size or number of clutches per year, with which egg volume could trade off [12]. This mechanism cannot readily account for our findings, however, as sparrow-weaver mothers vary neither clutch size nor clutch number according to helper numbers (see Results and Supplementary materials B). Additional analyses also suggest that maternal plasticity in egg volume cannot be readily attributed to carry-over effects on maternal condition of helper actions in previous breeding attempts (see Supplementary materials C - F).

While the ‘differential allocation hypothesis’ does predict the pattern of plasticity in pre-natal investment observed here (mothers increase egg volume when helped), the observed pattern of plasticity in post-natal investment (mothers *decrease* nesting provisioning rate when helped) runs counter to that recently predicted under differential allocation [9]. In general terms, the differential allocation hypothesis proposes that mothers should increase maternal investment under circumstances that increase their return on investment in the current breeding attempt, such as having a more attractive mate or more helpers [6,24]. Accordingly, models that apply this rationale specifically to pre-natal investment in cooperative breeders (by having the mother’s return on pre-natal investment per offspring increase when she has help with post-natal care; [9]), predict that mothers should increase both their pre- *and* post-natal investment per offspring when helped. These predictions are consistent with the patterns observed in the only other species to date in which mothers are thought to consistently lay larger eggs when they have more help: Iberian magpie mothers with helpers appear to lay larger eggs *and* provision their nestlings at higher rates than those without helpers ([22,25]; but whether either reflects maternal plasticity is unknown). It is notable then that sparrow-weaver mothers instead increase pre-natal investment per offspring while *decreasing* post-natal investment per offspring when helped (i.e., engage in ‘maternal front-loading’). Despite this discord, it would seem premature to rule out a role for differential allocation in the maternal strategy observed here, as the relevant theoretical work to date [9] might not capture all relevant aspects of the biology at play. For example, as per the differential allocation rationale, sparrow-weaver mothers might increase egg size with female helper number because the additive post-natal care that their female helpers will provide [35] increases the mother’s expected return on investment per egg (e.g., producing larger hatchlings may yield a greater payoff when they stand to be fed at higher rates [9,10]). Such additive post-natal care by helpers [35] is accompanied here by mothers decreasing their own post-natal contributions when helped; a maternal strategy of post-natal 'partial compensation' commonly observed in cooperative breeders [8]. As such, modifications to existing models to incorporate, or more fully explore, the selective pressures that favour such maternal post-natal compensation (e.g., strongly diminishing returns of post-natal care [8,40]), could conceivably leave the differential allocation rationale predicting the maternal strategy observed here (i.e., differential allocation at the egg stage accompanied by maternal post-natal compensation). The integration of stronger maternal trade-offs between pre- and post-natal investment and/or higher costs to mothers of post-natal investment might also resolve the apparent discord.

Differential allocation rationale could conceivably explain the maternal investment strategy observed here (see above); however, our findings do highlight a simpler explanation for sparrow-weaver mothers laying larger eggs when helped. The differential allocation hypothesis envisages that helpers increase the maternal *benefit* of pre-natal investment per offspring (e.g., via the provision of additive post-natal care; [9]). However, helpers may instead reduce the maternal *cost* of pre-natal investment per offspring by reducing maternal post-natal workloads. Maternal front-loading may therefore reflect an anticipatory strategy in which the expected lightening of maternal *post-natal* workloads allows helped mothers to focus their investment on the *pre-natal* phase, to which helpers cannot contribute directly. Such a maternal strategy may therefore be of particular benefit when pre-natal investment has differentially large effects on offspring fitness. Under this scenario, the maternal increase in egg investment when helped is a consequence of the helper effect on the mother's post-natal workload, whereas under the differential allocation hypothesis the increase is typically considered a product of the additive effect of helpers on the overall provision of post-natal care [6,10,15,22]. Species in which helpers lighten maternal post-natal workloads but do *not* have additive effects on post-natal care (because the maternal reduction in post-natal work rate completely compensates for helper contributions [8]) would therefore provide a fruitful testing ground for these alternative, though not mutually exclusive, hypotheses. As helpers frequently lighten maternal post-natal workloads in cooperative breeders [5,8,40,41], the maternal front-loading strategy observed here could ultimately prove more commonplace once more studies formally characterize maternal plasticity in egg investment [12]. For example, recent evidence suggesting that superb fairy-wren mothers with helpers lay larger eggs than those without when conditions are warm [10] could reflect maternal front-loading in warm conditions, if the reported population-level relationship between egg size and the availability of help arose via maternal plasticity, and if post-natal load-lightening also occurred under such warm conditions (which it might [42]). While red-winged fairy wren mothers do not increase egg size when helped, they do show a plastic increase in clutch size when helped [12]; another form of maternal front-loading that could arise via the same mechanism: helpers reducing the cost of egg investment by lightening the mother's post-natal workload [43].

Where mothers do front-load their investment per offspring to the pre-natal stage when helped (as observed here), post-natal helping may have hitherto unexplored beneficial effects on the pre-natal development of offspring. The potential for such cryptic 'pre-natal helper effects' has important implications for attempts to identify and quantify the benefits of helping in cooperative societies. First, while it has been suggested that studies of helper effects on offspring should control for variation in egg size in order to ensure that maternal *reductions* in egg size by helped mothers do not 'conceal' helper effects on offspring [5], our findings highlight a danger of this approach. If, as here, mothers lay *larger* eggs when helped, controlling for variation in egg size could lead to the *underestimation* of helper effects on offspring, by factoring out helper effects that arise indirectly via maternal investment in the egg. Second, while helper-induced reductions in maternal post-natal workloads are typically thought to benefit mothers (e.g., by improving maternal survival; [5,8]), our findings highlight that associated changes in egg investment could pass these benefits, in part or whole, to the offspring being reared. Indeed, as helpers commonly lighten maternal post-natal workloads [8,40–42], a maternal front-loading response of the type observed could conceivably have contributed to the positive relationships already described in numerous species between helper numbers and offspring survival or performance.

Our findings provide formal evidence of maternal plasticity in pre-natal investment per offspring according to the availability of help in a natural population [29]. They reveal a plastic maternal pre-natal response that runs directly counter to the predictions of the leading load-lightening hypothesis and to general expectation given the limited empirical work to date [15]. The patterns of maternal plasticity in *post-natal* investment that we also document suggest that the overall maternal strategy does not match the existing predictions of the differential allocation hypothesis either [9], and instead highlight an alternative explanation for mothers increasing their egg size when helped: by lightening maternal post-natal workloads, helpers may allow mothers to focus their investment on the pre-natal stage, to which helpers cannot contribute directly. The novel ‘maternal front-loading’ strategy that sparrow-weaver mothers appear to employ has important implications for attempts to both identify and quantify the benefits of helping, the best-studied form of animal cooperation.

Materials and Methods

General Field Methods

White-browed sparrow-weavers live in semi-arid regions of East and Southern Africa. Our study population is located 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 April between 2007 and 2016 inclusive. Approximately 40 social groups were monitored, each defending a small exclusive territory within an overall study site of approximately 1.5 km^2. Sparrow-weaver groups were easily monitored and distinguished in the field as all group members foraged together, engaged in communal weaving and territory defense, and roosted within in a single tree or cluster of trees close to the center of their territory. All birds in the study population were fitted with a single metal ring and three color rings for identification from the time they were first detected in the population (under SAFRING license 1444). The sex of each bird could be determined after six months of age using the sex difference in bill color [44].

Each social group contains a single behaviourally dominant female. The dominant female is easily identified in the field because she displays a distinct set of behaviours: being behaviourally dominant to other females, being the only female observed to incubate the eggs or enter the nest during the incubation phase, and closely associating with and frequently duetting with the dominant male [45]. Genetic analyses have confirmed that the dominant female is always the mother of any eggs or chicks produced on their group's territory; subordinate females never breed [33]. For brevity, we therefore refer throughout the paper to the dominant female as the 'mother'.

Each group's territory was regularly monitored (every one or two days while nests were present) to detect new clutches. Once a new clutch was found, egg length and maximum width were measured with a plastic calliper to the nearest 0.1 mm. Nests were then checked daily until the clutch had been completed. Clutches were then checked 8 days after the first egg was laid (to confirm the progression of incubation), before daily checks were resumed 15 days after the first egg was laid, until the fate of every egg had been determined (hatch or failure). Hatchlings were weighed on their first day of life using a portable scale to the nearest 0.01 g.

The composition of each social group was assessed every week throughout each field season, with birds being identified on the basis of their color-ring combination. Birds were also routinely caught while roosting within their group’s territory at night, and this information also contributed to group composition assessments. Group compositions were typically very stable over time, with group members residing within the same social group for many months to many years at a time (i.e., group composition not being affected by short-term fluctuations in environmental conditions). For every breeding attempt in our analyses, we used these group compositions to calculate the number of male and female helpers that the dominant female (mother) had on the day of laying (for the egg volume analyses) and on the days that provisioning behaviour was recorded (for the maternal provisioning rate analyses). All subordinate group members over the age of 6 months were considered helpers, as analyses of helper contributions suggest that subordinates < 6 months old contribute little to nestling provisioning [34,46].

Nestling provisioning behaviour

Nestling provisioning behaviour was recorded between September 2007 and April 2016. We collected provisioning data using video recordings of the birds visiting the nest (viewed from below the nest) between the 10th and 12th day inclusive after the first egg of a given clutch had hatched (this is the period of highest nestling post-natal demand; the nestling period lasts approximately 20-25 days). At least five days before video recording started, we (i) caught and marked the vent of each group member other than the dominant female using hair dye [35] to aid their identification on the video and (ii) deployed a tripod on the ground beneath the nest to acclimatize the birds to its presence prior to recording. On recording days, the video camera was set up and recording started soon after sunrise, at standard times relative to sunrise in order to track seasonal changes in sunrise timings. Provisioning behaviour was recorded for approximately three hours per day per brood. Video recordings were then watched using VLC media player to determine the rate at which each group member visited the nest (here after their ‘provisioning rate’), identifying each visitor via their sex (based on bill coloration [44]), unique vent pattern and color-ring combination. Prior analyses using within-nest cameras have confirmed that during this peak provisioning period all nest visits by all group members entail the delivery of a single food item by the visitor that is then eaten by the chicks (the only exception being nest-maintenance visits that were easily excluded from the data set on the basis of the visitor conspicuously carrying grass [47]).

We then calculated the provisioning rate of mothers (feeds / hour). In some cases, we were unable to reliably identify every visiting bird within the provisioning video, yielding some uncertainty in our estimate of maternal provisioning rate. We therefore only carried forward maternal provisioning rate estimates to our statistical analyses where the maximum possible maternal provisioning rate (i.e., if one considered the mother the feeder in *all* cases of uncertain feeder identity) did not exceed the observed maternal provisioning rate (calculated solely on the basis of the mother's identified visits) by more than 3 feeds / hour. Applying this filtering criteria, there was less than 10% uncertainty for more than 90% of maternal provisioning rate estimations. Where estimates of maternal provisioning rate were available for multiple mornings for a given breeding attempt, the measures were averaged to yield a single mean maternal provisioning rate for each breeding attempt for analysis (as maternal provisioning rate estimates for a given breeding attempt were highly correlated over successive mornings of video recording). This yielded a data set for analysis of mean maternal provisioning rate for 50 different dominant females (mothers) feeding 124 broods in 34 social groups.

Environmental data

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

Temperature data for a 0.25 degree latitude x 0.25 degree longitude area that encompassed the study site was extracted from the GLDAS-2.1 Noah 0.25 degree 3-hourly data set [48], accessed via the NASA's Goddard Earth Sciences Data and Information Services Center online data system (Giovanni; http://disc.sci.gsfc.nasa.gov/giovanni). From this, we calculated the daily maximum temperature and daily mean temperature (i.e., the average of all eight measures available per 24 hour period) for all days of our study. The daily mean temperatures from this data set were highly correlated with those obtained directly within our study site using a 2700 Watchdog weather station (Spectrum Technologies Inc) deployed for part of the study period (partial coverage of 2010-2015; Pearson's product-moment correlation: r = 0.973, 95%CI = 0.970 – 0.975, df = 1,771).

Statistical analysis

Modelling egg volume effects on egg mass and hatchling mass within and among-mothers

First, we investigated whether egg volume and egg mass were correlated and whether egg volume predicted hatchling mass. To this end, we fitted linear mixed models to (i) explain variation in egg mass (g) and (ii) hatchling mass (g) including egg volume as a fixed effect predictor. These models also included mother ID as a random intercept. Both models were fitted a second time to partition the effect of egg volume on each of the response variables within- and among-mothers (see details below), to investigate whether variation in egg volume within mothers (i.e., plasticity) was associated with variation in egg mass and hatchling mass (i.e., providing evidence for the biologically relevant role of plasticity in egg volume).

Modelling maternal pre-natal investment per offspring: egg volume

Linear mixed models with Gaussian error structure were used to investigate the predictors of egg volume (measured in cm^3 and calculated based on length and maximum breadth following the formula given in [49]). Four terms were included as random intercepts: breeding season (referring to each of the nine different September-April breeding seasons studied), social group ID, clutch ID and maternal ID. The following were included as fixed effect predictors: egg position within the clutch, clutch size, number of female helpers, number of male helpers and the interaction between helper number (both females and males) and (i) egg position, and (ii) clutch size. These interactive terms are included to specifically test whether the effect of helpers on egg volume is dependent on egg position or clutch size. To control for the potential effects of temperature and rainfall on egg volume, we also fitted the following two indices as fixed effect predictors: a 'heat waves' index (the number of days in which the maximum daily temperature exceeded 35°C within a time window spanning the 13 days prior to egg laying) and a rainfall index (the total rainfall that fell within a time window spanning 44-49 days prior to egg laying). The specific time windows used for the calculation of these indices were determined objectively by the application of a sliding window approach prior to this modelling step (see Supplementary materials A). The 'heat waves' index as defined here (i.e., number of days above 35°C) has been shown to appropriately capture hot-weather events in the Kalahari and it impacts the reproductive biology of several Kalahari bird species [50,51]. Egg position, clutch size and heat waves index were standardised (i.e., mean centered and divided by one standard deviation) prior to model fitting to facilitate model convergence. Similarly, to improve model convergence, orthogonal polynomials of degree two (i.e., quadratic effects) were calculated to model quadratic effects of rainfall index but model estimates were back transformed for presentation purposes and provided in change of egg volume (cm^3) per 100 mm of rainfall. Between 2007 and 2016 inclusive, we collected egg length and width information (and therefore volume) from 906 eggs that were detected in the field with less than four days of uncertainty around their laying date. We focused our analysis on the 490 of these for which we also knew laying order (allowing determination of the 'egg position within the clutch' variable): 490 eggs from 271 clutches laid by 62 dominant females (mothers) across 37 social groups (mean = 7.90 eggs per mother; median = 7 eggs per mother; range 1 – 21 eggs per mother; (Figure S6, Figure S7).

Modelling maternal post-natal investment: maternal nestling provisioning rate

Linear mixed models with Gaussian error structure were used to investigate the predictors of maternal provisioning rate (calculated as a single mean value for each breeding attempt; see above). Three terms were included as random intercepts: breeding season (see above), social group ID, and maternal ID. The following were included as fixed effect predictors: brood size, number of female helpers, number of male helpers and the interactions between helper number (both females and males) and brood size. These interactive terms are included to specifically test whether the effect of helpers is dependent on brood size. To control for the potential effects of temperature and rainfall on maternal provisioning rate, we also fitted the following two indices as fixed effect predictors: 'heat waves' index (the total number of days within a time window spanning 51-58 days prior to egg laying in which the maximum daily temperature exceeded 35°C) and a rainfall index (the total amount of rainfall that fell within a time window spanning 61-78 days prior to egg laying). The specific time windows used for the calculation of these indices were determined by the application of a sliding window approach prior to this modelling step (see Supplementary materials A). Brood size and heat waves index were standardised (i.e., mean centered and divided by one standard deviation) prior to model fitting to facilitate model convergence. Similarly, to improve model convergence, orthogonal polynomials of degree two (i.e., quadratic effects) were calculated to model quadratic effects of rainfall index but model estimates were back transformed for presentation purposes and provided in change of maternal provisioning rate (feeds / hour) per 100 mm of rainfall. The final data set contained 124 measures of mean maternal provisioning rate for 124 broods born to 50 dominant females (mothers) across 34 social groups. The data set contained more than one brood for 34 mothers, while 16 mothers were observed provisioning only once (Figure S7).

Modelling the effect of helper numbers on clutch size

Generalised linear mixed models with zero-truncated Poisson error structure were used to investigate the predictors of clutch size (range 1 to 3 eggs). Zero-truncated models were fitted using the R package glmmADMB (v0.8.3.3; [52]). Three terms were included as random intercepts: breeding season (referring to each of the nine different September-April breeding seasons studied), social group ID and maternal ID. The following were included as fixed effect predictors: clutch order within the breeding season (a continuous variable starting from 1 for the first clutch that a given mother laid within a given breeding season), number of female helpers and number of male helpers. The number of female and male helpers was calculated for the day on which the first egg of the focal clutch was laid (or the day at the mid-point of the window of potential lay dates for the first egg, whenever there was uncertainty regarding this lay date). The analysis used a data set of 344 clutches laid by 66 dominant females (mothers) across 37 social groups, all of which were found in the field with less than four days of uncertainty in the lay date of the first egg (reducing the probability that any egg in the clutch disappeared before we recorded it). Out of the 344 clutches, 284 (82.56%) were found on the day that the first egg was laid. There was one day of uncertainty regarding the first egg lay date for 37 clutches (10.76%), two days for 16 clutches (4.65%) and three days for 7 clutches (2.03%).

Modelling the effect of helper numbers on the number of clutches laid per year.

Generalised linear mixed models with Poisson error structure were used to investigate the predictors of the number of clutches that mothers laid per year (calculated as the number of clutches laid by each mother during each breeding season, running from 1st September in one calendar year to 30th April in the next; see above). For this analysis, we only used data from females that were dominant for the whole breeding season (208 clutch numbers for 56 dominant females [mothers] across 38 social groups). Two terms were included as random intercepts: social group ID and maternal ID. The following were included as fixed effect predictors: the mean number of female and male helpers during the focal breeding season (the average for the period 1st September to 30th April) as well as the total rainfall that fell during the focal breeding season.

General statistical procedures

We built models that included fixed effect variables and interactions predicted to have an effect on the focal response term (see above for details; these were always chosen *a priori* based on biological hypothesis) and evaluated the statistical importance of predictors in these models via likelihood-ratio tests (LRT). If not statistically significant, interactive terms were removed from initial models to ease the interpretation of the effects of non-interactive terms. We provide tables of results for these full models including effect sizes (i.e., model coefficients, estimate), effect size standard errors (‘SE’), model coefficient 95% confidence intervals (‘95% CI’), and likelihood-ratio test results (χ^2 value, degrees of freedom of the test and p-value (Tables 1-4). We complemented this statistical approach with another analysis based on AIC model selection. Briefly, we fitted all possible models containing simpler combinations of fixed effect predictors and ranked them for model fit based on Akaike’s Information Criterion (AIC, [53]). We only fitted and AIC-ranked models that included a set of predictors hypothesised to have a biological effect on a focal response variable. With this approach, the best-supported model is the one with the lowest AIC value. ΔAIC values were then calculated for every model as the difference between the AIC of the focal model and that of the best-supported model. We report our results in the main text following the full-model approach and LRT outline above, and provide AIC model selection tables in Supplementary material (Tables S1-S8, including models with $\Delta AIC < 6$). Both approaches generate similar results and lead to the same conclusions. Our interpretation of the findings is robust to the choice of statistical framework. When interactive terms (e.g., quadratic terms) were included in a given model, the constituent single terms were always present. Model coefficients are reported and shown in their link-function scale and models were fitted using maximum likelihood. We formally tested for differences in the effects of male and female helper numbers (i.e., testing whether the slopes of these two predictors are statistically different) using Wald χ^2 tests implemented in the R package ‘car’ (v3.1.0; [54]) via its ‘linearHypothesis’ function. Normality and homoscedasticity of model residuals was inspected visually in all models. Statistical analyses were performed in R version 4.2.1. [55], and (unless otherwise specified) statistical models were fitted using the R package ‘lme4’ (v1.1.29; [56]).

General statistical procedures: partitioning among-mother and within-mother (i.e., plasticity) effects of helpers

A common concern in studies of the effects of helper numbers on fitness-related traits in cooperative species is that positive correlations between the two could arise not from a causal effect of helpers on the focal trait but instead from both helper numbers and the focal trait being positively impacted by territory (and/or maternal) quality [57,58]. We addressed this concern in two ways. First, we excluded young individuals (< 6 six months old) from our calculations of the number of male and female helpers (see above; as they contribute little to helping), given that transient resource peaks could leave recent and current productivity positively correlated, potentially yielding a spurious correlation between helper number and current productivity if recently fledged young were considered helpers. Second, we first carried out our analyses using the number of (male and female) helpers as the focal predictor, and then partitioned this variable into its within- and among-mother components: Δ (male or female) helper number and μ (male or female) helper number respectively [32]. 'μ helper number' is the mean 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 clutch or brood and 'μ helper number'. This approach allows us to statistically isolate the effects 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), which are indicative of maternal *plasticity*, in the knowledge that its effects cannot be attributed to variation in quality *among* mothers or their territories. A recent study has shown that partitioning within- and among-individual effects following this approach provides a robust estimation of the within-individual effect size, the parameter of most interest in this study [59]. We formally tested for statistical differences between among-mother and within-mother effects (i.e., statistical difference in the slopes of these two variables) applying Equation 3 in [32].

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Figures and Tables

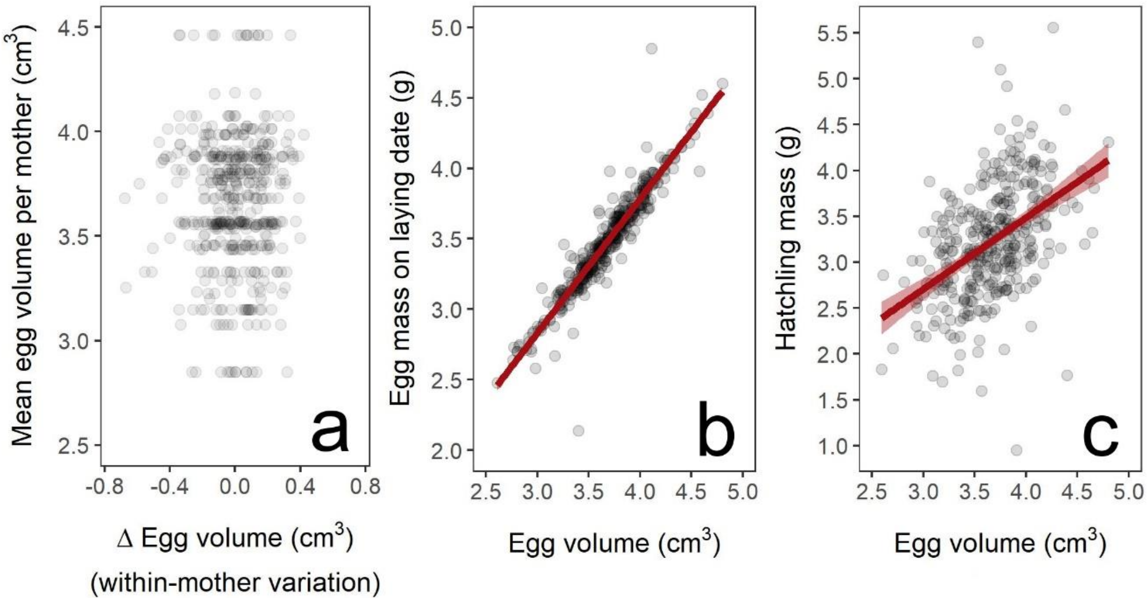

Figure 1. Patterns and implications of maternal variation in egg volume. (a) Egg volume showed high variation both within (x-axis) and among mothers (y-axis). Δ egg volume represents the difference in egg volume between the focal egg and that mother's own mean egg volume (i.e., within-mother variation; hence the negative and positive values). (b) Variation in egg volume positively predicted egg mass (g) on the day of laying (effect size ± Standard Error [SE] = 0.951 ± 0.018 g / cm^3; N = 391 eggs with volume and laying mass data; $\chi^2_1 = 625.98$, $p < 0.001$) and (c) nestling mass (g) on the day of hatching (effect size ± SE = 0.679 ± 0.124 g / cm^3; N = 193 eggs with volume and hatchling mass data; $\chi^2_1 = 27.23$, $p < 0.001$). Mean model predictions ± standard error (SE) are plotted in red.

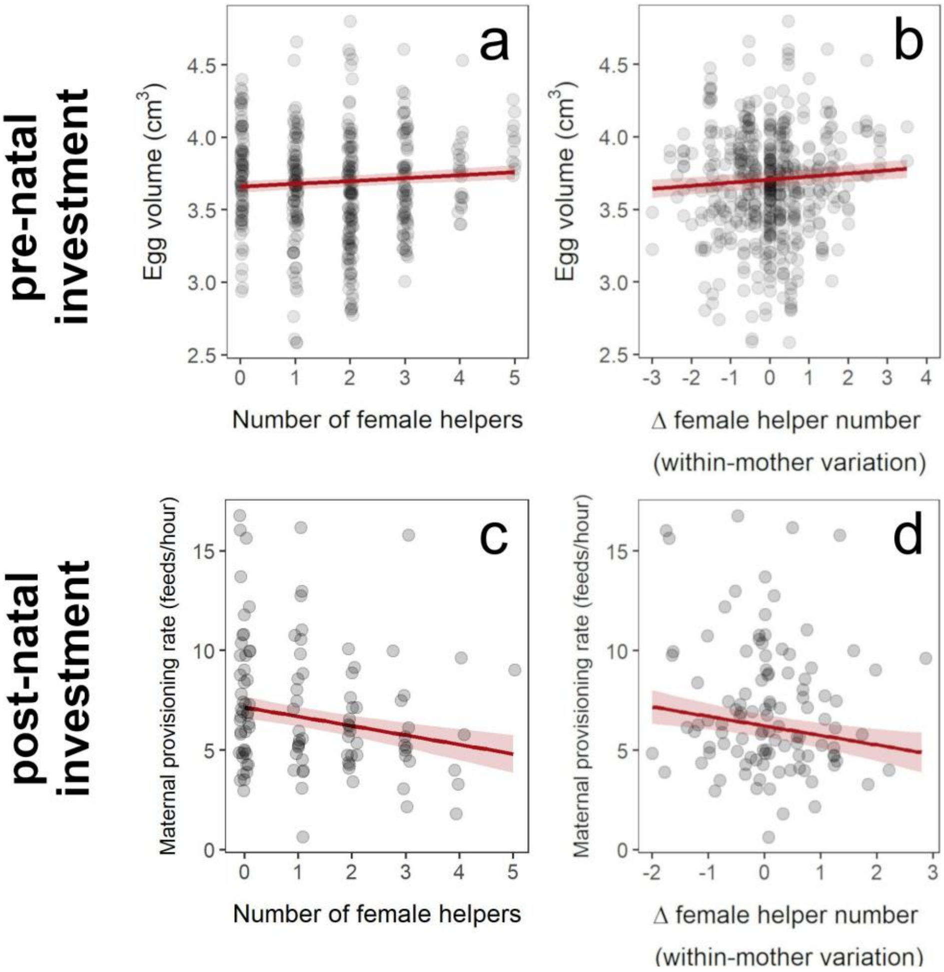

Figure 2. Maternal plasticity in pre-natal (egg volume) and post-natal (nestling provisioning rate) investment according to female helper numbers. (**a**) Female helper number positively predicts egg volume at the population level (Table 1; prior to partitioning variation in helper number). (**b**) Within-mother variation in female helper number ('Δ female helper number') also positively predicts egg volume, providing evidence of maternal plasticity (see results, Table 2 and Table S2). (**c**) Female helper number negatively predicts maternal nestling provisioning rate at the population level (Table 2). (**d**) Within-mother variation in female helper number ('Δ female helper number') also negatively predicts maternal nestling provisioning rate, providing evidence of maternal plasticity (see result, Table 4 and Table S4). Grey dots illustrate raw data points and red lines present model predictions (± SE).

Table 1. Summary of results of a linear mixed model explaining variation in egg volume (cm^3) and including every main effect of interest (N = 490 eggs laid in 271 clutches by 62 mothers in 37 social groups; 1-21 eggs [median = 7] measured per mother). Model estimates, standard errors (SE) and their 95% confidence intervals (CI (95%)) are provided along with results from likelihood-ratio tests ($\chi^2_{df = 1}$ and associated p-values) assessing the statistical significance of each predictor within the full model (i.e., a model containing all of the terms in the table below). Random effect standard deviation: 'season' = 0 cm^3, 'group ID' = 0 cm^3, 'clutch ID' = 0.070 cm^3, 'mother ID' = 0.275 cm^3. 'Heat waves' (days above 35˚C), 'Clutch size' and 'Egg position' were mean centered and scaled by one standard deviation prior model fit to improve model convergence. Estimates for 'Rainfall^1' and 'Rainfall^2' given for 100mm of rainfall (e.g., change in egg volume [cm^3] per 100mm of rainfall). 'df' = degrees of freedom for likelihood-ratio tests. This analysis yielded the same conclusions when taking an AIC-based model selection approach (Table S1).

Predictors	**Estimates**	**SE**	**CI (95%)**	**χ^2_1**	**p-value**
Intercept	3.630	0.039	3.553, 3.707	-	-
Rainfall^1	0.310	0.116	0.082, 0.538	-	-
Rainfall^2	-0.005	0.001	-0.007, -0.002	15.46	< 0.001
Heat waves	-0.042	0.010	-0.061, -0.023	17.89	< 0.001
Number of female helpers	0.018	0.009	0.001, 0.035	4.31	0.038
Number of male helpers	0.008	0.010	-0.011, 0.026	0.61	0.435
Clutch size	0.001	0.011	-0.021, 0.023	0.01	0.918
Egg position	-0.043	0.009	-0.061, -0.026	23.20	< 0.001

Table 2. Summary of results of a linear mixed model explaining variation in egg volume (cm^3), including every main effect of interest when population-level variation in female and male helper number were partitioned into their within-mother (Δ) and among-mother (μ) components. Sample size and structure were identical to those for Table 1. Model estimates, standard errors (SE) and their 95% confidence intervals (CI (95%)) are provided along with results from likelihood-ratio tests ($\chi^2_{df = 1}$ and associated p-values) assessing the statistical significance of each predictor within the full model (i.e., a model containing all of the terms in the table below). Random effect standard deviation: 'season' = 0 cm^3, 'group ID' = 0 cm^3, 'clutch ID' = 0.070 cm^3, 'mother ID' = 0.275 cm^3. 'Heat waves' (days above 35°C), 'Clutch size' and 'Egg position' were mean centered and scaled by one standard deviation prior model fit to improve model convergence. Estimates for 'Rainfall^1' and 'Rainfall^2' given for 100mm of rainfall (e.g., change in egg volume [cm^3] per 100mm of rainfall). 'df' = degrees of freedom for likelihood-ratio tests. This analysis yielded the same conclusions when taking an AIC-based model selection approach (Table S2).

Predictors	**Estimates**	**SE**	**CI (95%)**	χ^2_1	**p-value**
Intercept	3.641	0.051	3.540, 3.741	-	-
Rainfall^1	0.313	0.116	0.084, 0.542	-	-
Rainfall^2	-0.005	0.001	-0.007, -0.002	15.58	< 0.001
Heat waves	-0.042	0.010	-0.061, -0.023	17.77	< 0.001
Δ Number of male helpers	0.008	0.010	-0.012, 0.028	0.57	0.450
μ Number of male helpers	0.008	0.029	-0.048, 0.065	0.09	0.769
Δ Number of female helpers	0.019	0.009	0.001, 0.037	4.36	0.037
μ Number of female helpers	0.009	0.028	-0.045, 0.063	0.10	0.755
Egg position	-0.043	0.009	-0.061, -0.026	23.18	< 0.001
Clutch size	0.001	0.011	-0.021, 0.023	0.01	0.909

Table 3. Summary of results of a linear mixed model explaining variation in maternal provisioning rate (feeds / hour) and including every main effect of interest (N = 124 broods being fed by 50 mothers in 34 social groups; 1-7 broods [median = 2] per mother). Model estimates, standard errors (SE) and their 95% confidence intervals (CI (95%)) are provided along with results from likelihood-ratio tests ($\chi^2_{df = 1}$ and associated p-values) assessing the statistical significance of each predictor within the full model (i.e., a model containing all of the terms in the table below). Random effect standard deviation: 'season' = 0.97 feeds / hour, 'group ID' = 0 feeds / hour, 'mother ID' = 0 feeds / hour. 'Heat waves' (days above 35˚C) and 'Brood size' were mean centered and scaled by one standard deviation prior model fit to improve model convergence. Estimates for 'Rainfall^1' and 'Rainfall^2' given for 100mm of rainfall (e.g., change in maternal provisioning rate [feeds / hour] per 100mm of rainfall). 'df' = degrees of freedom for likelihood-ratio tests. This analysis yielded the same conclusions when taking an AIC-based model selection approach (Table S3).

Predictors	Estimates	SE	CI (95%)	$\chi^2_{df=1}$	p-value
Intercept	7.460	0.537	6.325, 8.559	-	-
Rainfall^1	-7.974	4.055	-16.117, 0.218	-	-
Rainfall^2	0.201	0.072	0.057, 0.345	7.34	0.007
Heat waves	0.699	0.302	0.092, 1.296	5.03	0.025
Number of female helpers	-0.457	0.195	-0.841, -0.073	5.39	0.020
Number of male helpers	-0.072	0.228	-0.530, 0.381	0.10	0.754
Brood size	1.438	0.244	0.952, 1.920	30.02	<0.001

Table 4. Summary of results of a linear mixed model explaining variation in maternal provisioning rate (feeds / hour), including every main effect of interest when population-level variation in female and male helper number were partitioned into their within-mother (Δ) and among-mother (μ) components. Sample size and structure were identical to those for Table 3. Model estimates, standard errors (SE) and their 95% confidence intervals (CI (95%)) are provided along with results from likelihood-ratio tests ($\chi^2_{df = 1}$ and associated p-values) assessing the statistical significance of each predictor within the full model (i.e., a model containing all of the terms in the table below). Random effect standard deviation: 'season' = 0.92 feeds / hour, 'group ID' = 0 feeds / hour, 'mother ID' = 0 feeds / hour. 'Heat waves' (days above 35˚C) and 'Brood size' were mean centered and scaled by one standard deviation prior model fit to improve model convergence. Estimates for 'Rainfall^1' and 'Rainfall^2' given for 100mm of rainfall (e.g., change in maternal provisioning rate [feeds / hour] per 100mm of rainfall). df' = degrees of freedom for likelihood-ratio tests. This analysis yielded the same conclusions when taking an AIC-based model selection approach (Table S4).

Predictors	**Estimates**	**SE**	**CI (95%)**	**$\chi^2_{df=1}$**	**p-value**
Intercept	7.445	0.641	6.130, 8.750	-	-
Rainfall^1	-8.042	4.053	-16.164, 0.127	-	-
Rainfall^2	0.203	0.072	0.059, 0.347	7.50	0.006
Heat waves	0.713	0.302	0.105, 1.310	5.21	0.022
Δ Number of female helpers	-0.559	0.269	-1.090, -0.027	4.24	0.040
μ Number of female helpers	-0.325	0.304	-0.928, 0.287	1.14	0.285
Δ Number of male helpers	0.006	0.307	-0.601, 0.612	<0.01	0.986
μ Number of male helpers	-0.188	0.408	-1.042, 0.620	0.21	0.646
Brood size	1.446	0.244	0.959, 1.928	30.26	< 0.001