Helpers increase the reproductive potential of offspring in cooperative meerkats

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In both animal and human societies, individuals may forego personal reproduction and provide care to the offspring of others. Studies aimed at investigating the adaptive nature of such cooperative breeding systems in vertebrates typically calculate helper 'fitness' from relationships of helper numbers and offspring survival to independence. The aim of this study is to use observations and supplemental feeding experiments in cooperatively breeding meerkats, *Suricata suricatta*, to investigate whether helpers influence the long-term reproductive potential of offspring during adulthood. We show that helpers have a significant and positive influence on the probability that offspring gain directs reproductive success in their lifetimes. This effect arises because helpers both reduce the age at which offspring begin to reproduce as subordinates and increase the probability that they will compete successfully for alpha rank. Supplemental feeding experiments confirm the causality of these results. Our results suggest that one can neither discount the significance of helper effects when none is found nor necessarily estimate accurately the fitness benefit that helpers accrue, unless their effects on offspring are considered in the long term.

Keywords: early conditions; helper effects; fitness; kin selection; lifetime reproductive success

1. INTRODUCTION

Understanding the evolution of cooperative breeding systems, wherein individuals help to rear offspring that are not their own, relies fundamentally on understanding the fitness benefits that individuals accrue from helping. In the majority of studies on cooperative vertebrates, estimations of helper fitness have been based on the effects of helper number/investment on offspring survival to independence (Emlen 1991; Jennions & Macdonald 1994; Cockburn 1998; Russell 2004). However, recent evidence from non-cooperative vertebrate species has revealed that levels of parental investment not only influence the survival of dependent offspring, but also their reproductive potential and longevity during adulthood (Lindström 1999; Lummaa & Clutton-Brock 2002). Such findings are of importance to our understanding of the adaptive nature of vertebrate cooperative breeding systems, because helper investment can rival or even succeed the importance of parental investment as the primary determinant of offspring growth and condition (Hatchwell 1999). If helpers also have long-term survival and reproductive consequences for the offspring that they help to rear, then calculations of helper fitness based on short-term measures of offspring survival during dependence could lead to underestimations of the fitness benefits that individuals accrue from helping, and a reduced understanding of the strength of selection on, and the evolution of, breeding cooperatively.

The potential for helpers to have positive effects on offspring beyond the age at which those offspring reach independence is clear. In humans (Lahdenperä *et al.* 2004) and long-tailed tits, *Aegithalos caudatus* (Hatchwell *et al.* 2004), non-breeding grandmothers and failed-breeding adults, respectively, are associated with an increase in the probability that independent offspring survive to adulthood. Indeed, the study by Hatchwell *et al.* (2004) is of particular note because they failed to detect an effect of helpers on the number of offspring raised to independence. While other studies have used similar findings to question the adaptive nature of helping, Hatchwell *et al.* (2004) found that, by improving offspring mass at fledging, helpers have dramatic effects on the probability that independent offspring survive to breed. However, whether helpers additionally influence the reproductive potential of offspring that reach adulthood (as studies on non-cooperative vertebrates would suggest) has not been considered previously, although Solomon (1991) demonstrated that helpers influence the weight of offspring at weaning in prairie voles (*Microtus ochrogaster*), and that heavy offspring are preferred as social mates during adulthood (Solomon 1993) and are more fecund as breeders (Solomon 1994). The overall aim of this study is therefore to use observational and supplemental feeding data in free-ranging meerkats (*Suricata suricatta*) to investigate the effect of helpers on the lifetime reproductive success of offspring in a cooperative vertebrate.

Meerkats are small (less than 1 kg) cooperatively breeding mongooses that live in groups of approximately

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15 individuals (range 2–50) in arid regions of southern Africa. Groups comprise overlapping generations of first- and second-order kin (mean $r = 0.3$) in which a dominant pair is responsible for the majority of reproduction (Clutton-Brock *et al*. 2001*a*; Griffin *et al*. 2003; Russell *et al*. 2003*a*). Dominant females deliver up to three litters per year of three to six pups per litter. Pups are born below ground, and during the first month are guarded by helpers at the burrow and are reliant on milk supplied by their mother and allo-lactators (Clutton-Brock *et al*. 2002, 2003; Scantlebury *et al*. 2002). From one month, pups join the group on forays and are fed invertebrates and small vertebrates by group members until independence at three months (Brotherton *et al*. 2001). Offspring begin to contribute to cooperation from independence, but contributions by those under six months old are low (Clutton-Brock *et al*. 2002). Helping can be associated with growth costs, but is apparently associated with little or no long-term fitness costs (Russell *et al*. 2003*b*). From 1 year, subordinate female helpers can attempt to outbreed with immigrant or roving males in and around their natal group, while subordinate male helpers prospect in search of breeding opportunities in neighbouring groups (Clutton-Brock *et al*. 2002; Young *et al*. 2005). Females can attain dominance in their natal group on the death of the current dominant, males can disperse and compete for dominance in established groups, while either sex can disperse and compete for dominance in new groups.

Helpers are known to have a number of effects on both the reproductive output of the dominant female (Russell *et al*. 2003*a*) as well as the growth and survival of all offspring born in the group (Clutton-Brock *et al*. 2001*b*; Russell *et al*. 2002). Helper number is positively associated with the number of litters that dominant females deliver per year and is weakly associated with the number of offspring that emerge from such deliveries. However, helpers do not appear to be associated with greater pup weights at weaning, presumably because contributions by allo-sucklers are not additive to that of the mother (Scantlebury *et al*. 2002). By contrast, helpers have considerable additive effects on the amount of food delivered to all weaned pups, their growth rates during post-weaning development and their ultimate weight at independence. Manipulations of helper : pup ratios confirm that increases in relative helper numbers cause increases in pup weight gain. Finally, helper number is positively associated with the survival of weaned offspring during their first year of life. In this study, we use eight years of observational and supplemental feeding data to investigate the effect of helpers on: (i) the probability that offspring gain directs reproductive success in their lifetimes, (ii) the underlying life-history traits that influence offspring reproductive probability (i.e. probability of breeding as a subordinate and of obtaining alpha rank), and (iii) a potential mechanism responsible for differences in offspring lifetime reproductive probabilities.

2. MATERIAL AND METHODS

Our study population (established in 1993) is located in South African Kalahari ranchland (26°58′ S, 21°49′ E). Habitat and climate are published elsewhere (Russell *et al*. 2002). The present study uses data collected primarily between 1996 and 2003. During this period, all groups ($n = 12$) were visited for up to 7 h per day every 1–5 days with the following data being recorded: group size (number of individuals greater than three months old); number of dependent pups (number of individuals less than three months old); individual pregnancy and dominance status (alpha or not); as well as all births, deaths, dispersal events and male prospecting events (temporary extra-group forays in search of reproductive opportunities). All individuals were individually recognizable, fully habituated to observers (from less than one month) and most could be weighed before foraging each day using crumbs of hard-boiled egg to entice them onto electronic balances (± 1 g). Descriptions of such data collection have been published previously (Clutton-Brock *et al*. 2001*a*, 2002, 2004, 2005; Young *et al*. 2005).

Investigating long-term helper effects is not straightforward. Helper number may represent a poor predictor of helper effects, since helpers can vary substantially in their contributions to offspring provisioning (Heinsohn 2004; Russell 2004). In addition, pups that are raised by many helpers during dependence can be in large groups post-dependence, and so any long-term effect of helpers is not easily dissociated from any benefits of simply being in a large group post-dependence (Jennions & Macdonald 1994). We resolve these problems in two ways. First, we use pup weights at independence as a surrogate for helper effects after statistically removing non-helper effects. Second, we use supplemental feeding experiments to substantiate the causality between offspring weight at independence and future success. The effects of both helper-mediated pup weights at independence and supplemental feeding on the long-term fitness prospects of pups can then be analysed using linear mixed-model analyses controlling for group size post-independence and repeated measures within litters, mothers and groups.

Meerkat pups are fully independent by three months of age (Brotherton *et al*. 2001). Morning, pre-foraging, weights ($n = 4170$) collected when pups ($n = 408$) were 91–120 days old were used to calculate helper-mediated pup weights at independence. Besides the effects of helpers, pup weights at independence are influenced by their age (91–120 days), environmental conditions (rainfall and temperature) and maternal effects pre-weaning (maternal weight; Russell *et al*. 2002). We determined the mean helper-mediated weight of pups at independence by removing statistically the effects of mean pup age at independence (91–120 days), total rainfall and mean maximum daily temperature during their period of dependence, and maternal effects. (Maternal effects were removed using the weight of pups at one month: one month represents the age at which pups begin to be weaned and to receive solid food from helpers; Brotherton *et al*. 2001). Pups with negative and positive weight residuals were then categorized as having received less than average helper input (hereafter referred to as light) and greater than average helper input (hereafter referred to as heavy), respectively. Parental input to pup provisioning could not be dissociated from helper inputs, but this is unlikely to represent a significant bias since litters are reared by varying the numbers of helpers and seldom varying the numbers of parents.

Supplemental feeding experiments were used to substantiate the effect of pup weight at independence on all traits analysed. Supplemental feeding experiments involved feeding random samples of pups with an average of 12 g of hard-boiled hens' eggs twice per day for 38 days during development. Fed pups were compared with unfed pups

from the same litter and from the litter immediately before and/or immediately after it, if born to the same mother in the same group and within six months. Pups fed supplementally were excluded from all analyses investigating the effects of pup weights at independence.

(a) *Helper effects on lifetime reproductive probability*
In our population of meerkats, 83% of offspring that reached independence ($n=213$) died/disappeared before successfully rearing any offspring of their own. Consequently, the effects of both helper-mediated pup weights at independence and supplemental feeding on the lifetime reproductive success of offspring had to be analysed as a probability. Therefore, our definition of lifetime reproductive success is whether or not offspring produced their own offspring to weaning before their death/disappearance. Whether or not females successfully reared offspring was known with precision (Griffin *et al.* 2003), while male success was determined using microsatellite fingerprinting of 14 polymorphic loci (see electronic supplementary material). Included in the analyses of lifetime reproductive probability are all those pups that were born more than 18 months before the end of the study (i.e. had the potential to survive to breeding age), reached independence and died/disappeared before the end of the study. Overall, the age at death/disappearance ranged from 4 months to 5 years old (mean=2 years, $n=213$), but their potential ages ranged from 18 months to 6 years old (mean=4 years).

Obviously, such an analysis relies to a certain degree on knowledge of whether individuals that disappeared dispersed out of our study population successfully or died. Individuals that disappeared without showing prior dispersive tendencies are likely to have died, while the success of long distance dispersal is likely to be very low (Stephens *et al.* 2005). In this study, 50% of individuals included in the analysis were known to have died or bred before they disappeared, while the rest are assumed to have died. It is acknowledged that a lack of perfect information regarding the eventual success of dispersers is a potential shortcoming of this part of our study, although it is unlikely to lead to substantial bias (see §4). In addition, restriction of the analysis to include only those individuals that were known to have died led to qualitatively similar results, but we believe significantly overestimates our fitness estimates quantitatively.

The effect of both helper-mediated pup weights at independence and supplemental feeding on the probability that individuals gained reproductive success in their lifetimes were analysed using two separate generalized linear mixed models (GLMM; see §2*d* for details). Whether or not offspring produced any surviving offspring of their own in their lifetimes was fitted as a binomial response term in each. Pup weight at independence or whether or not pups were supplementally fed were fitted as the main fixed effects in each of the two models, respectively, while pup sex (both analyses) and mean group size between independence and death (correlational analysis) were fitted as a covariates to control for post-independence group size effects. Litter, maternal and group identities were fitted as random terms in both the analyses to control for repeated measures across error terms (Schall 1991). Our analysis of the effect of pup weight was based on 181 offspring for which lifetime reproductive data were available. These offspring were born in 89 litters (1–6 measures per litter) to 36 mothers (1–26 measures per mother) in 12 groups (1–33 measures per group). Our analysis of the effect of supplemental feeding was based on

114 offspring. These offspring were born in 52 litters (1–6 measures per litter) to 15 mothers (1–23 measures per mother) in 9 groups (2–23 measures per group).

(b) *Helper effects on underlying life-history traits*
We investigated the effect of both helper-mediated pup weights at independence and supplemental feeding on three key life-history traits that may underlie fitness: the probability that offspring attempted to breed and/or disperse before average age, and the probability that they competed successfully for alpha rank.

The probability that subordinate females became pregnant by 2 years of age and the probability that subordinate males began prospecting to neighbouring groups in search of mating opportunities by 18 months were used to determine both the effect of weight at independence and of supplemental feeding on the age at which pups began attempting to breed as subordinates. These ages represent (to the nearest six months) when 50% of the subordinate individuals have become pregnant (females) and prospected (males). Female pregnancy is easily determined visually after the first of their two and half-month gestation period, with the reliability of this method having been confirmed using ultrasound imaging (Clutton-Brock *et al.* 2001*a*). Male-prospecting forays are also obvious, with males leaving their group for an average of 3 days and often satelliting neighbouring groups (Young *et al.* 2005). Analyses were restricted to include only those pups that were known to have survived to 2 years of age (females) and 18 months of age (males). Again, two separate GLMM analyses were conducted, one for pup weights and one for the supplemental feeding experiment. In each analysis, the probability that an offspring had attempted to breed was fitted as the response term, while sex (both analyses) and mean group size between independence and the age in question (correlational analysis) were fitted as covariates. Litter, mother and group identities were fitted as random terms in both the analyses. In the pup weight analysis, we obtained data for 200 individuals (88 females, 112 males) born in 87 litters (1–6 measures per litter) to 35 mothers (1–27 measures per mother) in 10 groups (1–33 measures per group). In the supplemental feeding experiment, we obtained data for 117 individuals (52 females, 65 males) born in 58 litters (1–7 measures per litter) to 19 mothers (1–18 measures per mother) in 9 groups (8–34 measures per group).

The probability that offspring dispersed by 2 years of age was used to investigate the effect of both weight at independence and supplemental feeding on dispersal behaviour. This age represents (to the nearest six months) when 50% of the subordinate individuals have attempted to disperse. Dispersal is defined as being attempted if individuals left their group and were either known to have dispersed into a new group or disappeared *en masse* (meerkats usually disperse in groups of greater than or equal to three individuals) and never returned (Stephens *et al.* 2005). Cases where only one individual disappeared were categorized as death since meerkats rarely disperse alone (Clutton-Brock *et al.* 2002). The analysis was restricted to include only those pups that had survived to 2 years of age. Again, two separate GLMM analyses were conducted, one for pup weights and one for the supplemental feeding experiment. In each analysis, the probability that an offspring had dispersed by 2 years was fitted as the response term, while sex (both analyses) and mean group size between independence and 2 years (correlational analysis) were fitted as covariates. Litter, mother and group identities were fitted as random

terms in both the analyses. In the pup weight analysis, we obtained data for 178 individuals (88 females, 90 males) born in 71 litters (1–5 measures per litter) to 33 mothers (1–25 measures per mother) in 9 groups (3–28 measures per group). In the supplemental feeding experiment, we obtained data for 106 individuals (52 females, 54 males) born in 50 litters (1–6 measures per litter) to 17 mothers (1–14 measures per mother) in 9 groups (3–23 measures per group).

The effect of pup weight at independence on an offspring's probability of competing successfully for alpha rank was analysed by comparing the weight at independence of 23 individuals that competed successfully for alpha rank with the weight of 23 unsuccessful competitors (litter mates ($n=8$) or those competitors most closely matched for age (older $n=6$ and younger $n=9$), if within six months of age). Ages did not differ between successful (median$=747$ days old) and unsuccessful (median$=773$ days old) competitors (Wilcoxon matched pair test $W=14.00$, $N=23$, $P=0.72$). The proportion of supplementally fed and unfed individuals that competed successfully versus unsuccessfully for alpha rank was used to examine the effects of being fed on the probability of gaining alpha rank. Fed and unfed individuals were viewed as competitors if in the same group when a change in dominance was observed, if they were aged within six months of each other and if they were over 2 years old. Ages did not differ between fed and unfed competitors (Mann–Whitney U-test, $W=262$, $N=15,23$, $P=0.37$). The sexes were combined in both analyses due to low sample sizes.

(c) The mechanism of helper effects

The simplest explanation for long-term helper effects is that the probability that individuals gain reproductive success in their lifetime is size-dependent, and helper-mediated size benefits gained during early development are maintained into adulthood. In order to test this idea, we investigated whether: (i) weight advantages at independence are maintained into adulthood, and (ii) weight at 1 year of age replaces the importance of weight at independence as the primary predictor of the probability that individuals gained reproductive success in their lifetimes. In these analyses (unlike those above), weight at independence was used rather than helper-mediated weight at independence, because it is not possible to measure the helper-mediated weight of individuals during adulthood.

To investigate whether or not weight advantages at independence are maintained into adulthood, we first used a residual maximum likelihood model (REML) in which weight at 2 years of age was fitted as the response term (see §2*d*). The mean pup weight at independence was fitted as the primary fixed effect, while pup age at weighing, sex and mean group size between independence and 2 years (700–730 days old) were fitted as covariates. Litter, mother and group identities were fitted as random terms. Overall, we obtained adulthood weight data for 115 individuals born in 58 litters (1–5 measures per litter) to 28 mothers (1–17 measures per mother) in 9 groups (2–23 measures per group). Second, we substantiated this correlational analysis with our supplemental feeding experiments. In this case, we carried out four separate REML analyses corresponding to the effect of pup feeding status (fed or unfed) on pup weights at 3 months (90–120 days old), 6 months (180–210 days old), 12 months (330–360 days old) and 18 months (520–550 days old). Age and sex were fitted into each analysis as covariates, while litter ($n=59–46$), mother ($n=18–17$) and group identities

($n=9$) were fitted as random terms. Individual sample sizes are shown in the figures. Small sample sizes precluded analyses among 2-year olds in the experimental dataset.

(d) Statistical analyses

GLMM with binomial error structures and logit link functions and REML models with normal error structures were performed using GENSTAT 6 (Lawes Agricultural Trust, Rothamsted, Harpendon, UK). GLMM and REML models are similar to generalized and general linear models (GLM), respectively, except that they allow both fixed and random terms to be fitted, with random terms taking into consideration repeated measures across error terms (in this case: litters, mothers and groups; Schall 1991). Random terms were retained unless they constituted negative components of variance, indicating that they explained none of the variance in the model. Since the significance of a random term indicates whether or not variation between levels of the random factor differs significantly from variation within levels, their significance can be used as indicators of inherent differences between levels of the random factor. For example, in our analyses a significant random effect of maternal identity would suggest that some mothers are inherently more successful than others, suggesting that mothers vary significantly in their quality. The significance of a random term was estimated using its component divided by its standard error and comparing the resulting value to a t distribution with the degrees of freedom set as the number of levels within the random term minus the number of degrees of freedom taken up by the minimal model minus 1 for the constant. The significance of fixed terms in GLMM and REML analyses is presented as Wald Statistics which, in large datasets such as this one, approximate χ^2 distributions. In all GLMMs, the dispersion parameter was fixed at 1, as is appropriate for binomial (0, 1) scores. The residuals from all models were normally distributed (Kolmogorov–Smirnoff test $p>0.05$) and variances were homogenous (Levene's test, $p>0.05$). All interactions were tested between sex and either pup weight or supplemental treatment, but only presented if significant.

3. RESULTS
(a) Helper effects on lifetime reproductive probability

The probability that independent offspring gained reproductive success in their lifetimes was significantly and positively associated with the effect of helpers on their weight at independence (figure 1*a*). The magnitude of this effect equated to a more than twofold increase in the probability of gaining lifetime reproductive success between those that received high overall helper input when compared with those that received a lower overall input. The results of our supplemental feeding experiments substantiate the causality of the effect of weight at independence on the probability of gaining reproductive success in a lifetime. Supplementally fed pups, which were 25 g heavier at independence than unfed controls (see figure 3*a*), were three times more likely to gain reproductive success in their lifetimes than unfed controls (figure 1*b*).

(b) Helper effects on underlying life-history traits

Differences in the reproductive probability of light and heavy pups are likely to be generated by helper effects on a number of key offspring life-history traits. First, pups of both sexes
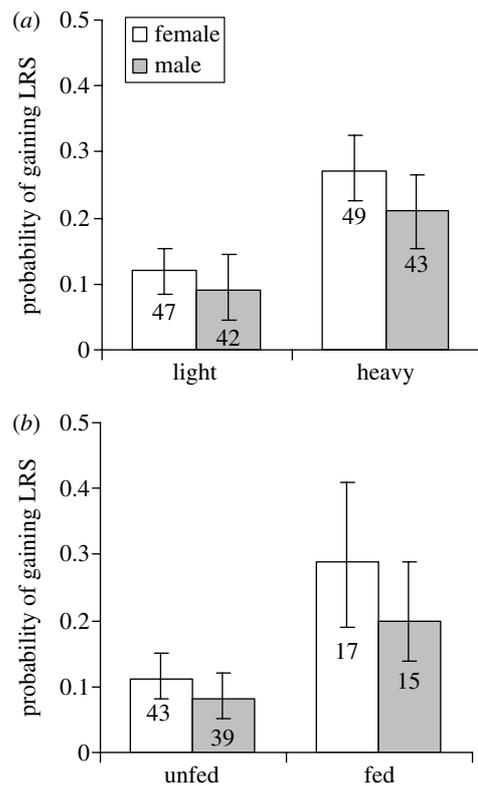
Figure 1. Effect of helper-mediated pup weights at independence and supplemental feeding on lifetime reproductive probability of offspring. Offspring that were (a) reared heavy at independence (GLMM: $\chi_1^2 = 5.87$, $p = 0.015$), and (b) supplementally fed during development (GLMM: $\chi_1^2 = 6.94$, $p = 0.008$) were significantly more likely to gain reproductive success in their lifetimes. Figures show predicted means (± 1 s.e.) for the sexes separately (overall sex effect, $p > 0.3$). Effects of group size ($p < 0.05$) were controlled in (a), while repeated measures were controlled in (a) and (b) (random terms: litter identity, $p < 0.05$; mother identity, $p > 0.5$; and group identity, $p > 0.9$). Values show number of individuals.

that were heavy at independence had a significantly higher probability of attempting to breed from a younger age as subordinates than those that were light at independence (figure 2a). Second, male pups that were heavy at independence were significantly more likely to disperse by 2 years of age than those that were light at independence, although there was a non-significant trend for the reverse effect among females (figure 2c), generating a significant interaction between offspring sex and weight at independence on dispersal probability (GLMM interaction term: $\chi_1^2 = 4.28$, $p = 0.039$). One explanation for this sex difference is that while males can only gain alpha rank by dispersing, females can also gain it in their natal group, leading to a dilution or reversal of selection on early dispersal among heavy females. Third, pups that were heavy at independence were twice as likely as similarly aged lighter rivals to compete successfully for alpha rank (figure 2e).

Again, the causality of these results is largely confirmed by our supplemental feeding experiments. Supplementally fed pups were significantly more likely to attempt breeding as subordinates from an earlier age than unfed controls (figure 2b). Fed males tended to disperse earlier than unfed males, while there was no apparent effect among females (figure 2d). Finally, a significantly greater proportion of fed offspring competed successfully for alpha rank than similarly aged unfed rivals (figure 2f).

(c) The mechanism of helper effects

The simplest explanation for our results is that the probability that individuals gain reproductive success in their lifetime is size-dependent, and size benefits gained during early development are maintained into adulthood. In accordance with this suggestion, weight differences between pups at independence were maintained, with pups that were significantly heavier at independence remaining so at 2 years of age (figure 3a). The causality of this result is confirmed by our supplemental feeding experiments. Fed pups were 25 g heavier than unfed controls at independence and were still 21 g heavier at 18 months of age (figure 3b).

However, the importance of this idea relies on showing that the inclusion of later life weight into the analysis of the lifetime reproductive probability has a significant effect at the expense of weight at independence. We only found partial evidence to suggest that this was the case. Among females, weight at 1 year of age replaced the importance of weight at independence as the primary predictor of the probability that individuals gained any reproductive success in their lifetimes (weight at 1 year effect, $\chi_1^2 = 7.82$, $p = 0.005$; weight at independence effect, $\chi_1^2 = 1.06$, $p = 0.31$, $n = 73$). However, this was not the case in males: weight at 1 year of age failed to account for significant variation in lifetime reproductive probability (weight at 1 year effect, $\chi_1^2 = 0.33$, $p = 0.57$), while weight at independence remained significant ($\chi_1^2 = 4.67$, $p = 0.031$, $n = 54$; see Clutton-Brock *et al.* in press).

4. DISCUSSION

Levels of parental investment can have profound effects on the reproductive potential of offspring in non-cooperative vertebrates. Here we show that this is also the case of overall levels of helper investment in a cooperatively breeding vertebrate. In meerkats, helper-mediated pup weights at independence were significantly associated with the probability that pups would gain direct reproductive success in their lifetimes. This effect arose because pups that were raised by helpers in good condition were more likely to breed at a younger age as subordinates and to compete successfully for alpha rank. The most parsimonious explanation for these results is that an individual's reproductive potential during adulthood is size-dependent and that size advantages at independence are maintained into adulthood. We found evidence to support this idea in females, but not in males.

Helper investment influenced the probability that independent offspring gained direct reproductive success in their lifetimes. This result is unlikely to be confounded by group size post-independence, or either maternal or territory quality. Group size post-dependence was controlled in the analysis, and the probability that pups gained reproductive success in their lifetimes was not systematically biased towards certain mothers or territories (maternal and territory identity constituted non-significant random terms ($p > 0.5$) in all models (see §2d)). In addition, helper-mediated pup weights at independence were not significantly different between mothers (GLM, $F_{35,144} = 1.49$, $p = 0.060$) or groups (GLM, $F_{11,169} = 1.63$, $p = 0.083$), although trends appeared to exist. Finally, the results
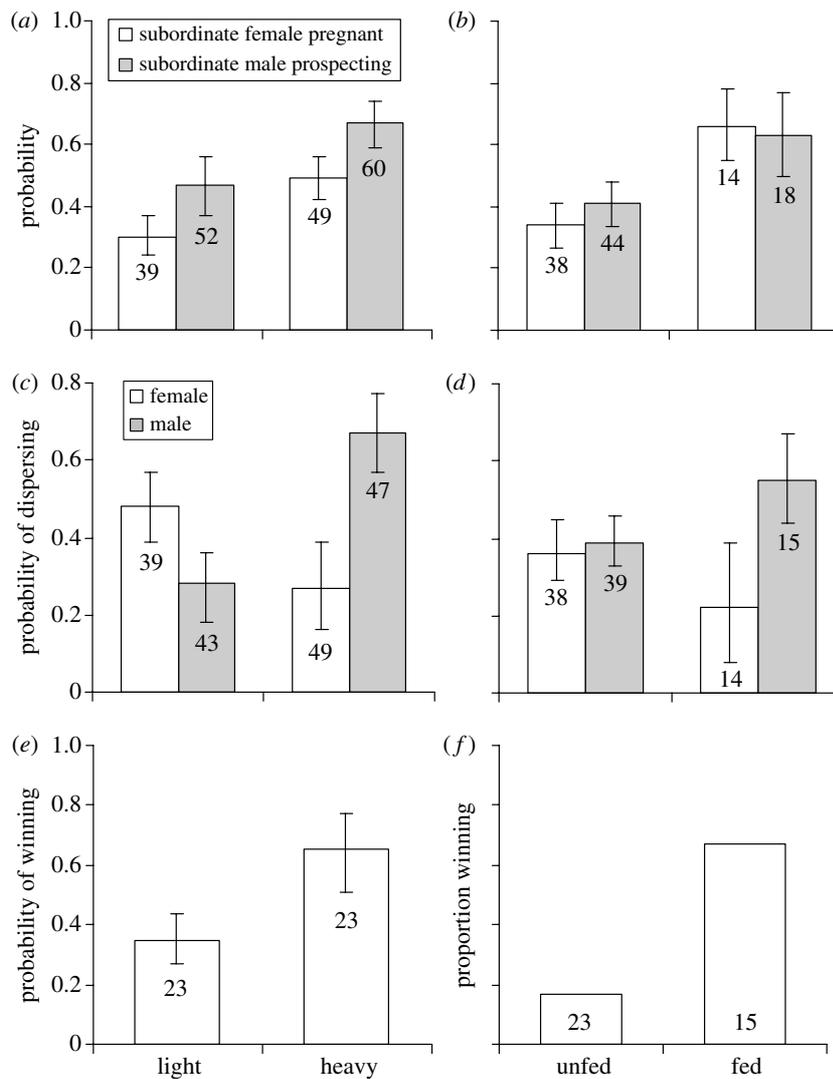
Figure 2. Effects of helper-mediated pup weights at independence and supplemental feeding on underlying offspring life-history traits. Helper-mediated weight at independence was positively associated with the probability that: (a) offspring attempted to breed early as subordinates (GLMM for females, $\chi_1^2 = 7.10$, $p = 0.008$; GLMM for males, $\chi_1^2 = 4.67$, $p = 0.031$); (c) males ($\chi_1^2 = 5.18$, $p = 0.023$), but not females ($\chi_1^2 = 1.55$, $p = 0.21$) will have dispersed by 2 years of age; and (e) offspring competed successfully for alpha rank (Paired t-test, $t_{22} = 2.40$, $p = 0.025$). Supplemental pup feeding was positively associated with: (b) the probability that offspring attempted to breed early as subordinates (GLMM for females, $\chi_1^2 = 8.38$, $p = 0.004$; GLMM for males, $\chi_1^2 = 5.19$, $p = 0.027$); (d) the probability that males ($\chi_1^2 = 3.11$, $p = 0.078$), but not females ($\chi_1^2 = 0.02$, $p = 0.88$) dispersed by 2 years of age; and (f) the proportion of individuals that competed successfully for alpha rank (G-test $= 9.47$, d.f. $= 1$, $p = 0.002$). Values show number of individuals. (a–d) Show predicted means (± 1 s.e.), after controlling for any significant effects of group size and random terms (litter identity ($p < 0.05$), mother identity ($p > 0.5$) and group identity ($p > 0.9$).

of our supplemental feeding experiments confirm that differences in pup weights cause the differences in fitness and not the differences in the above potential confounds.

Second, the result could be confounded by dispersal if light individuals are as likely to gain success as heavy ones, but have to disperse to do so. This is highly unlikely. Although complicated by differential sex effects, we found no overall evidence to suggest that lighter (GLMM, $\chi_1^2 = 1.13$, $p = 0.29$) or unfed ($\chi_1^2 = 0.62$, $p = 0.43$) offspring have greater dispersive tendencies. In addition, for females, dispersal is extremely costly; they never disperse voluntarily and we found that light females are less likely to breed as subordinates and to compete successfully for alpha rank. Although males do disperse voluntarily, we found that heavy (not light) males dispersed first, roved in search of breeding opportunities earlier and competed more successfully for alpha rank. Finally, if dispersal represents a significant problem, we might expect our estimate of fitness for philopatric females to be significantly different than for dispersive males. This was not the case: 18% of females bred successfully before death/disappearance, while this value was 12% for males ($\chi_1^2 = 1.86$, $p = 0.17$).

Helper influences on key life-history traits of offspring were likely to have influenced the probability that pups gain direct reproductive success in their lifetimes. We have shown previously that helper number is associated with the probability that pups survive their first year of life (Clutton-Brock *et al.* 2001b). This effect is insufficient to account for our results. First, inclusion of only those pups that survived to the mean age at which reproduction is first attempted (females, 2 years; males, 18 months) showed that pups that were heavy at independence and those that were supplementally fed were still significantly more likely to begin attempting to breed before the average age in the population. This effect is likely to be important: few individuals ever attain alpha rank and subordinate females
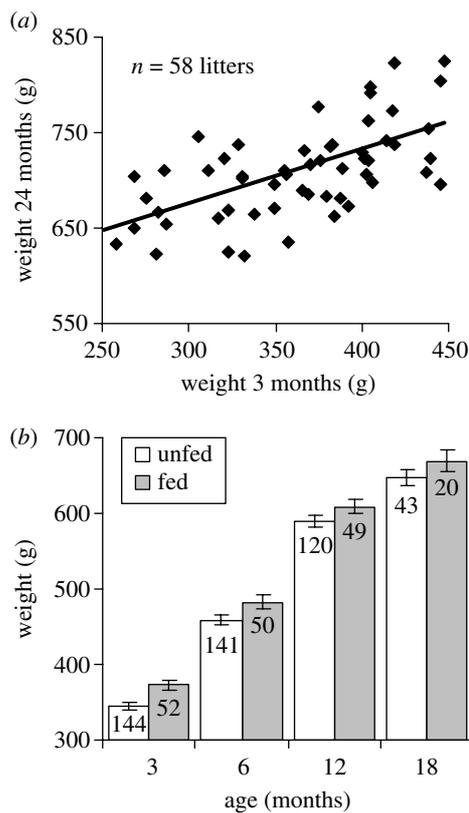
Figure 3. Weight at independence and its maintenance into adulthood. (*a*) Weight at independence is positively correlated with weight at 2 years (REML: $\chi^2_1 = 36.29$, $p < 0.001$). (*b*) Pups that were supplementally fed during development are heavier at independence (REML: $\chi^2_1 = 24.11$, $p < 0.001$), 6 months ($\chi^2_1 = 6.79$, $p = 0.005$), 12 months ($\chi^2_1 = 5.11$, $p = 0.027$), and 18 months ($\chi^2_1 = 3.61$, $p = 0.057$). Figures show predicted means (± 1 s.e.) after controlling for average group size between independence and 2 years (*a*) and random terms (*a* and *b*) (litter identity, $p < 0.05-0.01$; mother and group identity, $p > 0.9$). Values show number of individuals.

delivered 17% of all emergent pups, while prospecting males sired 16% of emergent pups delivered by dominant females and 45% of emergent pups delivered by subordinate females. Second, pups that were heavy at independence and those that were supplementally fed were significantly more likely to compete successfully for alpha rank when opportunities arose, than were similarly aged rivals that had been lighter at independence. This effect is likely to be of substantial importance, for 83% of all emergent pups were delivered by the alpha females in a group, while alpha males fathered 70% of these pups and 23% of those delivered by subordinate females.

Evidence from non-cooperative vertebrate species shows that levels of nutrition received during early development can have profound effects on an individual's reproductive potential during adulthood (Lindström 1999; Lummaa & Clutton-Brock 2002), and that individuals which receive a poor start in life are unable to compensate later (Metcalfe & Monaghan 2001). There is also some evidence to suggest that this is the case in cooperative vertebrates. In humans, helping grandmothers have been shown to increase the probability that grand-offspring survive to adulthood (Lahdenperä *et al.* 2004), and grandmothers are known to increase the dietary intake of dependent grand-offspring (Sear *et al.* 2000). In long-tailed

tits, helpers increase the probability that offspring survive to adulthood, and helpers are known to increase chick weight through increased provisioning, and heavy chicks are known to survive better post-independence (Hatchwell 1999; Hatchwell *et al.* 2004). Finally, Solomon (1991) used experiments in prairie voles to show that helpers have a significant positive effect on the weight of offspring at weaning, and those that are heavy at weaning were subsequently shown to be preferred as social partners (both the sexes; Solomon 1993) and more fecund as breeders (females; Solomon 1994).

We have demonstrated previously that helpers have a significant positive effect on the biomass intake rates of dependent pups as well as their rate of growth and weight at independence (Clutton-Brock *et al.* 2001*b*; Russell *et al.* 2002). In addition, we have also shown that the reproductive potential of adult female meerkats is weight and size-dependent (Clutton-Brock *et al.* 2001*a*; Russell *et al.* 2003*a*, 2004). Consequently, the most parsimonious explanation for our results is that differences in reproductive potential during adulthood are caused by helper-mediated size/weight advantages at independence being maintained into adulthood. That we found that weight advantages at independence are maintained into adulthood in this study is consistent with this idea. However, a more comprehensive test is to examine whether weight during adulthood replaces the importance of weight at independence in the analysis of lifetime reproductive probability. If differences in reproductive probability are simply a consequence of maintenance of weight advantages into adulthood, we would predict that weight during adulthood would replace the importance of weight at independence as the primary predictor of reproductive probability. We found that this was the case in females, but not in males (see also Clutton-Brock *et al.* in press). This suggests that the more parsimonious mechanism outlined above is operating in females, but suggests that in males early developmental conditions influence reproductive potential independently of their influence on current body weight. Why this should be the case is currently unclear.

That helpers can influence the later-life survival and reproductive capacities of offspring has at least two important implications. First, the use of short-term measures of helper effects could lead to significant underestimations of the force of selection acting on cooperation and a misunderstanding of the adaptive nature of breeding cooperatively (see also Hatchwell *et al.* 2004). As a consequence, where the estimates of helper effects are based on observations of (or experiments on) offspring survival pre-independence, one can neither discount the significance of helper effects when none is found nor accurately estimate the fitness benefit accrued by helpers even when an effect is found. Second, groups of cooperative vertebrates have been suggested to be highly susceptible to extinction when they fall below a threshold group size (Courchamp *et al.* 1999). Studies suggest that such Allee effects arise owing to poor breeding success and adult survival in small groups. This study suggests that a further significant factor can be the poor reproductive capacity of offspring reared in small groups.

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