

Benefits of cooperation in captive Damaraland mole rats

Thomas M. Houslay*¹, Philippe Vullioud¹, Markus Zöttl^{1,2}, Tim H. Clutton-Brock^{1,3}

* Corresponding author: houslay@gmail.com

¹ Department of Zoology, University of Cambridge, Cambridge, CB2 3EJ, UK

² EEMiS, Department of Biology and Environmental Science, Linnaeus University, SE-391 82 Kalmar, Sweden

³ Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, 0028 Pretoria, South Africa

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Abstract

Although the social mole rats are commonly classified as eusocial breeders on the grounds that groups include a single breeding female (the 'queen') and a number of non-breeding individuals ('helpers') of both sexes, alloparental care is not highly developed in these species and there is no direct evidence that the presence or number of non-breeders is associated with reductions in the workload of the 'queen'. An alternative interpretation of mole rat groups is that the social mole rats are cooperative foragers rather than cooperative or eusocial breeders. Here, in captive colonies of Damaraland mole rats (*Fukomys damarensis*), we provide the first evidence that increases in the number of nonbreeding subordinates in mole rat groups are associated with reductions in the workload of 'queens' and with increases in their fecundity.

Introduction

The social mole rats are regularly classified as the only eusocial vertebrates (e.g., Jarvis 1981; Jarvis and Bennett 1993; Jarvis et al. 1994; Burda et al. 2000) on the grounds that they meet Wilson's three criteria for eusociality (Wilson 1971; Wilson 2000): that individual colony members cooperate in caring for the young; that there is reproductive division of labour; and that there is an overlap of at least two generations in life stages capable of contributing to colony labour. Both of the two social mole rats whose behaviour has been described in detail (naked mole rats, *Heterocephalus glaber*, and Damaraland mole rats, *Fukomys damarensis*) live in sizeable groups where a single female monopolises reproduction, and groups include individuals from several different generations, so that they satisfy Wilson's second and third criteria (Sherman et al. 1991; Bennett and Faulkes 2000). However, it is uncertain whether they meet the first criterion, as alloparental care is not well developed in the social mole rats. Non-breeding subordinates do not provision pups with food, although pups do beg for and ingest faeces from adults (Jarvis 1981; Bennett 1990), which may provide them with the gut flora required for digesting cellulose (Jarvis 1991). Non-breeders will retrieve offspring from the tunnel system and return them to the nest or remove pups from the nest during disturbances (Bennett and Jarvis 1988; Jarvis 1991), although such events are usually rare (Zöttl et al. 2018). The principal collective activity of non-breeding 'helpers' is to maintain the extensive network of tunnels that provide access to the underground tubers of the plants that colony members feed on and to bring food to one or more stores that are accessible to all group members (Brett 1991; Bennett and Faulkes 2000). As all

group members are likely to benefit from this, their behaviour does not necessarily fall within the usual definition of cooperative breeding, which requires evidence that the activities of helpers are adapted to increasing the reproductive success of breeders or the survival of their offspring (West et al. 2007; Clutton-Brock 2016).

In many 'singular' cooperative breeders (i.e., where a group has one dominant or breeding female), the presence of non-breeding subordinates is associated with reductions in the work load of 'queens' and with increases in their fecundity (Clutton-Brock 2016; Koenig and Dickinson 2016), but no studies have yet investigated whether similar associations occur in the social mole-rats. Although it has been suggested that non-breeding mole rats can be allocated to functional 'castes' that differ in size and behaviour (Bennett and Jarvis 1988; Bennett and Faulkes 2000), longitudinal studies of the development of individuals suggest that contrasts in behaviour between individuals are continuously distributed and that differences in behaviour between large and small individuals are a product of age-related variation in behaviour rather than of divergent developmental pathways or the presence of discrete castes (Jarvis et al. 1991; O'Riain and Jarvis 1998; Zöttl et al. 2016; Thorley, Mendonça, et al. 2018). As a result, it is still an open question whether the social mole rats should be regarded as either cooperative or eusocial breeders (Burda et al. 2000) rather than as social foragers (Lacey and Sherman 2007; Clutton-Brock 2016).

A first step in determining whether mole rats should be regarded as cooperative breeders is to investigate whether the presence and activities of non-breeding

group members is associated with reductions in the workload of breeders or with increases in their fecundity. Increases in group size and helper number have been shown to be associated with increases in the fecundity of breeding females in several other mammals and birds that breed cooperatively (e.g., silver-backed jackals (*Canis mesomelas*; Moehlman 1979), African wild dogs (*Lycaon pictus*; Gusset and Macdonald 2010; Creel and Creel 2015), dwarf mongooses (*Helogale parvula*; Rood 1990), and superb fairy-wrens (*Malurus cyaneus*, Russell et al. 2007)). For example, in wild Kalahari meerkats, the contributions of breeding females to cooperative activities decline as the number of non-breeding helpers increases (Clutton-Brock et al. 2004) and the frequency of breeding attempts by dominant females rises (Russell et al. 2003), and similar effects have also been found in prairie voles (*Microtus ochrogaster*; Solomon 1991) and golden lion tamarins (*Leontopithecus rosalia*; Bales et al. 2001). As yet, there is no direct evidence of effects of this kind in social mole rats, though a mark-recapture study of wild Damaraland mole rats found higher rates of offspring recruitment in large groups relative to smaller ones (Young et al 2015). Studies of wild mole rats have been unable to investigate associations between the presence and activities of non-breeders with the workload and fecundity of non-breeders because these species are entirely fossorial and their behaviour cannot be observed directly.

Here, we use longitudinal data from over 55 captive groups of Damaraland mole rats to investigate whether larger groups (i.e., containing a greater number of non-breeders) are associated with reduced workload and increased resting and eating time of breeding females relative to non-breeders, and with greater

weight gain over gestation in breeding females. Within groups, over repeated breeding events we test whether greater cumulative contributions to collective activities by non-breeders are associated with lower workload, increased resting and eating time, and greater gestational weight gain in their breeding female. We also investigate whether larger groups are associated with increases in the breeding females' frequency of breeding and the size of their litters. As mole rat colonies are maintained with access to *ad libitum* food, we note that it is possible that effects of helper number that are present in naturally regulated populations are absent or undetectable in captive animals (e.g., Rothe et al. 1993; Yamamoto et al. 1996). The absence of effects of group size in captive colonies need not indicate that they are absent in wild animals too – though effects present in captive colonies are likely to underestimate their importance in natural populations.

Methods

Husbandry and data collection

We collected data from a captive population of Damaraland mole rats (either wild-caught or their offspring) maintained between February 2013 and June 2019 at the Kuruman River Reserve in the Northern Cape of South Africa. The starting population was captured within the reserve and on surrounding farmland between February and September 2013, and either maintained in their original capture group or used to establish new groups through pairing a single male and a female from different groups. The facility consists of seven temperature-controlled rooms containing 6-12 groups housed in artificial tunnel systems. Tunnel systems consist of 4-16 m of PVC tunnels (depending on group size) with transparent PET windows for behavioural observations, with compartments for nesting and food storage, latrines, and a single large box. Tunnel system sizes are classified depending on their shelf area footprint, and comprise 'small' (1 m²), 'medium' (2 m²) and 'large' (4 m²) systems. Groups are fed *ad libitum*, with sweet potatoes and cucumbers provided twice a day (with more food given than a group eats, and uneaten food removed regularly). Two to three vertical tunnels per system are refilled with clean sand twice a day for digging substrate. Tunnel systems are cleaned briefly on a daily basis, and more thoroughly every 2 weeks. Animals are identifiable on an individual basis through both a unique coloured dye mark applied to their white head patch and a passive integrated responder tag (PIT) implanted early in life. Individual body mass measurements are recorded weekly for those less than 90 days old, and every 2 weeks for older animals. Individuals are weighed on electronic scales

(Sartorius TE4100) after being manually removed from the tunnel system.

Individual sex can be determined from external genitalia (Seney et al. 2009).

We use behavioural data from instantaneous scan sampling (Martin and Bateson 2007) taken over 12 h observation periods ('scans'). Individual behaviours are recorded every 4 min using the Pocket Observer software (Noldus Information Technology, Wageningen, Netherlands) on a handheld Android device, yielding 180 sampling events per individual per scan. The ethogram covers 16 behaviours, and is described in more detail by Thorley *et al* (2018). During scan sessions, sand is added through the vertical pipes every 2 h to maintain the possibility of expressing foraging behaviour. The sand in our captive setup is relatively easy to move and is therefore more similar to conditions after rain, when sand is moist and digging less costly than under dry conditions (although is still energetically expensive; Lovegrove 1989; Jarvis et al. 1998; Scantlebury et al. 2006).

We cluster behaviours into categories of interest, and calculate total counts per individual per scan session. We define 'work' as the potentially mutualistic activities described by Thorley *et al* (2018), namely digging, kicking or sweeping sand, locomotion between episodes of those behaviours, transporting food, and nest building. We include resting, huddling and eating as 'rest+eat' behaviours. The remaining seven behaviours are excluded from our analysis, which also means that there is not necessarily a negative correlation between 'work' and 'rest+eat' within scan sessions.

Our overall data set includes 461 litters from 72 breeding females (ranging from 1 to 19 litters per queen). Variation in the number of litters and breeding females in each analysis (outlined in the following) is due to data collection schedules and removal of data entry errors prior to analysis. Here we limit the behavioural data to scans taken within the final 45 days of gestation, which comprises 3013 observations from 351 scans and includes 488 individuals across 170 litter events in 45 groups. The full maternal weight data set includes 5982 observations from the 90 days pre-parturition for 63 breeding females across 404 litters. 3632 of these observations are taken within the final 45 days of gestation and used in multivariate analyses (alongside behavioural data taken within the same time period). We include weight and scan data from groups in medium and large tunnel systems (i.e., 2 m² and 4 m²) only.

Statistical analysis

Previous studies have shown that measuring the effects of 'helpers' on breeder fitness faces substantial obstacles, such as the number of helpers being correlated with territory or breeder quality (Jennions and MacDonald 1994; Cockburn 1998; Woodroffe and Macdonald 2000; Eguchi et al. 2002).

Furthermore, individuals can vary widely in their contributions to helping (Bergmüller et al. 2010), making it difficult to use group size or helper number as a proxy for the overall level of 'helper' contributions. In our analysis we use several methods in an attempt to minimise these issues. By using mixed model analysis of repeated observations of queens over reproductive events, we account for variation among breeding females (or groups) in reproductive output and behaviour. We also use estimates of the cumulative workload of non-

breeders to examine their effect on the workload and reproductive success of breeding females, and use multivariate mixed modelling approaches to partition (co)variation among and within aspects of non-breeder and breeder behaviour and breeder weight gain during gestation.

We analysed all data with R version 3.6.1 (R Core Team 2019), and used the 'tidyverse' packages for data wrangling and visualisation (Wickham 2017). All analyses (univariate and multivariate) were fitted with generalised linear mixed models (GLMMs) in the R package MCMCglmm (Hadfield 2010). We use visual checks to assess model convergence and lack of autocorrelation among consecutive samples. We fit models with uninformative priors (with parameter expansion where possible for random effects), and checked that results are robust to different prior specifications and that multiple runs converge to similar results. For univariate models we used 260,000 iterations, a burn-in of 10,000, and retaining every 250th sample; for more complex multivariate models we used 510,000 iterations, a burn-in of 10,000, and retain every 50th sample. Fixed effects are considered significant if the 95% highest posterior density (HPD) credible intervals (CIs) exclude zero, and we also report pMCMC values (the probability that the posterior distribution includes zero). For multivariate models, we provide 95% HPD CIs for (co)variance estimates. Covariances and correlations are considered nominally significant if these 95% CIs do not cross zero.

Where we specify 'group size' as a predictor below, this denotes current group size at the time of observation. Where 'average group size' is used, this denotes

instead the geometric mean of group sizes across the 3 months preceding the observation. Tunnel system size has two levels (medium and large), and we include this as a continuous covariate centred at 0 with 1 unit of difference (i.e., medium = -0.5 and large = 0.5).

We analysed an individual's frequency of behaviours of interest (work, or resting and eating) during a scan session using separate MCMCglmm models fitted with an overdispersed Poisson error structure. For each model, the fixed effects comprised the breeding status of the individual (non-breeder, breeding female, breeding male), group size, and their interaction, in addition to covariates of the size of the current litter, individual's sex, whether the individual was less than 1 year old, and whether the starting time of the scan was in AM or PM. We also included random effects of individual ID, scan ID, litter ID (to group measures around a given reproductive event), and group ID.

We modelled cumulative behaviour of nonbreeding individuals with an overdispersed Poisson error structure, with fixed effects of average group size and random effects of litter ID (group ID was omitted as this explained negligible variation and produced poor diagnostics). The multivariate model of behaviour and weight gain in the 45 days pre-parturition included response variables of cumulative helper work per scan (Poisson), breeding female work per scan (Poisson), breeding female resting and eating per scan (Gaussian; centred and scaled to standard deviation units (1SDU)), and breeding female weight (Gaussian; centred and scaled to 1 SDU). We included a single fixed effect of the number of days into gestation (centred and scaled, and estimated for each trait

separately). In the random effects, we fit an unstructured covariance matrix at the litter level of the 4 response traits and a random regression of days into gestation (mean-centred and scaled to 1 SDU) on breeding female weight. We also fit an unstructured covariance matrix on the 4 response traits at the level of the group's breeding female, and at the residuals. We use the full data set to fit the model, and best linear unbiased predictors (BLUPs) for visualisation purposes only (Houslay and Wilson 2017).

We analysed the inter-birth interval (i.e., the number of days between successive litters, for breeding females that had at least 2 litters) using a Poisson model, with fixed effects of average group size (mean-centred), tunnel system size, and within-female litter sequence (mean-centred). We included a random regression of average group size on individual ID. For analysis of litter size, observations were underdispersed and we opted to use an ordinal model as Poisson error structure produced poor convergence diagnostics. Here we also included fixed effects of average group size (mean-centred), tunnel system size, and within-female litter sequence (mean-centred), and a random intercept for individual ID (as a random regression of average group size did not converge well, and appeared to explain no additional variance). Residual variance is not identifiable in the likelihood for ordinal models, and was fixed to 1 in the prior. Only one litter recorded greater than 6 individuals, and running the model excluding this data point made no qualitative difference to the results.

We analysed breeding female weight gain in the 90 days pre-parturition using a Gaussian error structure, with fixed effects of both linear and quadratic effects of

the number of days into gestation, and interactions between both of these and average group size (mean-centred). We included covariates of tunnel system size and within-female litter sequence (mean-centred). We allowed the age-related trend (both linear and quadratic) to vary among specific reproductive events (i.e., litter ID), and also included random intercepts of individual ID and group ID.

Results

As the number of non-breeding subordinates rises and group size increases, the cumulative contribution of non-breeders to all collective activities ('work') during the breeding female's pregnancy rises (group size effect = 0.15, 95% CI = [0.14, 0.17], pMCMC < 0.001; Figure 1A), while the average frequency with which individuals contribute to all collective activities ('individual work load') falls and the proportion of time individuals spend resting and eating rises (Figure 1B,C; Table 1A,B). Reductions in individual workloads and increases in the amount of time spent resting or eating were larger in 'queens' than in other group members.

Within groups (and among breeding events), when total contributions by non-breeders were large then queens worked less frequently, ate and rested more frequently, and gained weight more rapidly during the later stages of gestation (Figure 2, Table 2).

In larger groups, the inter-birth intervals of breeding females (the number of days between one litter and the next) is lower (average group size = -0.02, 95% CI = [-0.03, -0.01], pMCMC = 0.046; Figure 3A, Table S1) and their litter size is greater (average group size = 0.07, 95% CI = [0.00, 0.14], pMCMC = 0.045; Figure 3B, Table S2). Breeding females in larger groups also gained more weight during gestation (average group size \times days into gestation = 21.56, 95% CI = [15.24, 28.50], pMCMC < 0.001; average group size \times days into gestation² = 11.97, 95% CI = [8.00, 15.84], pMCMC < 0.001; Figure 3C, Table S3).

Discussion

As the size of mole rat groups and the cumulative contribution of non-breeders to collective activities increases, the workload of breeding females falls disproportionately (relative to that of individual non-breeders) and both their rate of weight gain during gestation and the size of their litters size rises, while the duration of intervals between obvious pregnancies decline and their fecundity increases. While the results we describe are correlative, the presence of consistent associations between increases in cumulative non-breeder workload and reductions in the workload of breeding females, increases in time they spend eating and resting, and increases in their weight gain during gestation – in addition to the strong relationship between group size and cumulative workload – suggest that the association between group size and female fecundity is based on a causal relationship. Since the animals in our captive groups were provided with food each day and their workload likely imposed lower costs relative to natural settings, stronger relationships between group size and female fecundity are to be expected in natural populations. Indeed, Burda *et al.* (2000) have suggested that the presence of non-breeding 'helpers' is necessary in social mole rats because breeding females are unable to store and mobilise enough fat reserves for prolonged gestation and lactation, and that breeding females are reliant upon regular provisioning of food by other group members.

Although sample sizes are too small for formal analysis, comparisons of the frequency of breeding by dominant females between the solitary and social

species of mole rat also indicate an association between social breeding and increases in breeding frequency (Table 3a), and a similar association between sociality and breeding frequency occurs among the social mongooses (Table 3b).

Our evidence that increases in the number and work load of nonbreeding subordinates are associated with reductions in the workload of breeding females and with increases in their fecundity suggests that the social mole rats are rightly regarded as cooperative breeders, despite their limited development of alloparental care. However, it is questionable whether they should be regarded as eusocial. Wilson's three criteria are now widely considered as an insufficient indication that species are eusocial since they would include a relatively large number of group living vertebrates not normally regarded as either cooperative or eusocial breeders, including many social primates, carnivores and cetaceans (Clutton-Brock 2016). Instead, many people working in this field follow Crespi & Yanega's (1995) suggestion that eusociality should be restricted to species where "individuals becomes fixed into one of [several] behavioural groups at some point prior to reproductive maturity, such that transitions from one behavioural group to [another] cannot and do not occur" (see also Boomsma and Gawne 2018). These criteria would exclude all vertebrates that breed cooperatively (including the social mole rats) for, although individuals may show irreversible morphological changes when they transition from being non-breeding helpers to being breeders (e.g., O'Riain et al. 2000; Thorley, Katlein, et al. 2018), there are no species where 'helpers' are permanently sterile, and no evidence of specialisation before maturity – and breeders can (and occasionally

do) revert to behaving as helpers if they lose their dominant status. Though the presence of helper castes has been suggested both for naked and Damaraland mole rats (e.g., Scantlebury et al. 2006), individual differences in the size and behaviour of non-breeding mole rats appear to be continuously distributed and to be a consequence of variation in age rather than of divergent developmental pathways (Jarvis et al. 1991; O'Riain and Jarvis 1998; Zöttl et al. 2016; Thorley, Mendonça, et al. 2018).

The absence of divergent pathways in early development and the presence of phenotypic adjustments after individuals acquire breeding status is probably connected to the importance of stochastic factors in determining whether individuals become breeders or remain as non-breeding helpers. In contrast to the divergent developmental pathways present in eusocial insects (e.g., O'Donnell 1998), female meerkats and mole rats that acquire dominant breeding positions subsequently show changes in hormonal status and behaviour as well as a secondary growth period, with the result that they are commonly the largest individual of their sex in their group (Bennett and Faulkes 2000; Clutton-Brock and Manser 2016). In many mammals that breed cooperatively, older females are killed or evicted by the breeding female and soon after her death the oldest or largest resident subordinate female inherits the breeding role – so the probability that individuals will acquire breeding status is strongly influenced by the time of the death of the last incumbent and is not predictable (Duncan et al. 2018). As a result, the evolution of divergent developmental pathways in young animals is unlikely to benefit their fitness and selection is more likely to favour

adaptive adjustments to the phenotype of individuals after they acquire breeding status (Duncan et al. 2018).

Our results also emphasise the diversity of cooperative behaviour and the problems associated with attempts to place species along a single continuum extending from facultative cooperators (where a relatively small proportion of breeding groups include one or more ‘helpers’) to eusocial breeders (where ‘queens’ are assisted by large numbers of obligately sterile workers that can be allocated to discrete tasks; Sherman et al. 1995; Boomsma and Gawne 2018). In many species that show cooperative behaviour (see Figure 4), individuals are likely to be involved in a variety of forms of cooperation, some of which are likely to generate direct fitness benefits while others probably generate indirect benefits and may have costs to the direct fitness of individuals. In some cases, the same cooperative activities may generate benefits of both kinds, as they probably do in the social mole rats.

As the number of cooperative breeding systems that have been studied increases, their diversity is becoming increasingly obvious (Beekman et al. 2006; Koenig and Dickinson 2016): for example, meerkats and dwarf mongooses (*Helogale parvula*) cooperate both to defend their territories and dig out sleeping burrows (‘mutualistic’ cooperation) and to act as sentinels and to feed and guard pups produced by the dominant female (‘altruistic’ cooperation) but do not forage cooperatively (Rasa 1987; Clutton-Brock and Manser 2016), while social mole rats cooperate to maintain foraging tunnels and store food but do not commonly feed or guard young born to other individuals, though they will groom

and return wandering pups to their nests (Bennett and Faulkes 2000). Contrasts in ecology, life histories and social organisation that affect the costs and benefits of cooperating (Figure 4) are likely to favour different forms and distributions of cooperation in different species rather than consistent differences in prosociality, so that we should be unsurprised to find that the tendency for individuals to cooperate is context-specific and that the distribution of cooperative behaviour among group members varies widely.

Such variation commonly reflects contrasts in ecology, life histories and social organisation and is not necessarily associated with differences either in the net benefits of cooperation or in levels of kinship. As a result, the 'eusociality continuum' envisaged by some (Sherman et al. 1995) is likely to be multi- rather than uni-dimensional, and we should anticipate the discovery of further variation in the contexts and distribution of cooperative behaviour rather than generalised differences in prosociality.

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Data Accessibility

Analyses reported in this article can be reproduced using the data provided by Houslay *et al.* (2020).

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Tables

Table 1: Effects of group size and individual status on average frequencies of (A) work, and (B) resting and eating per individual at times when the breeding female is pregnant. Estimates, 95% credible intervals and pMCMC values are given from separate MCMCglmm models (overdispersed Poisson and Gaussian respectively). Effects where 95% CIs exclude 0 are shown in bold.

Parameter	A. Work frequency			B. Resting + eating frequency		
	Estimate	95% CI	pMCMC	Estimate	95% CI	pMCMC
(Intercept)	2.905	2.81, 3.013	<0.001	126.8	123.3, 129.7	<0.001
Age class (<1 year)	-0.375	-0.445, -0.3	<0.001	5.003	3.293, 6.807	<0.001
Sex (Male)	0.023	-0.074, 0.124	0.644	1.744	-0.566, 4.155	0.148
Breeding male	0.052	-0.09, 0.188	0.538	0.026	-3.575, 3.551	0.998
Breeding female	-0.278	-0.426, -0.114	0.002	11.058	7.326, 15.058	<0.001
Group size	-0.031	-0.046, -0.016	<0.001	0.525	-0.004, 1.013	0.046
Time of day (PM)	-0.14	-0.289, 0.012	0.074	3.221	-2.414, 8.235	0.248
Breeding male × Group size	-0.012	-0.035, 0.016	0.392	0.307	-0.313, 0.979	0.334
Breeding female × Group size	-0.038	-0.062, -0.01	<0.001	1.142	0.520, 1.904	<0.001

Table 2: Relationships among traits within groups (among breeding events). Observations are taken from the period 45 days pre-parturition to parturition date. Trait variances are on the shaded diagonal, with covariances below and correlations above (95% credible intervals in parentheses). Correlations in bold denote those where 95% CIs exclude 0, and are considered nominally statistically significant.

	Cumulative non-breeder work	Breeding female work	Breeding female rest+eat	Breeding female weight	Breeding female weight gain
Cumulative non-breeder work	0.21 (0.14, 0.31)	-0.45 (-0.69, -0.16)	0.40 (0.11, 0.68)	-0.21 (-0.45, 0.01)	0.27 (0.05, 0.50)
Breeding female work	-0.09 (-0.16, -0.03)	0.20 (0.13, 0.32)	-0.93 (-0.99, -0.83)	-0.39 (-0.61, -0.13)	-0.45 (-0.62, -0.16)
Breeding female rest+eat	0.12 (0.03, 0.21)	-0.27 (-0.39, -0.17)	0.40 (0.26, 0.59)	0.38 (0.14, 0.59)	0.47 (0.23, 0.65)
Breeding female weight	-0.03 (-0.08, 0.00)	-0.06 (-0.11, -0.02)	0.09 (0.03, 0.15)	0.13 (0.11, 0.17)	0.53 (0.40, 0.61)
Breeding female weight gain	0.02 (0.00, 0.04)	-0.03 (-0.04, -0.01)	0.04 (0.02, 0.07)	0.03 (0.02, 0.03)	0.02 (0.02, 0.03)

Table 3: Annual breeding frequency of social and solitary species of (a) mole rats and (b) mongooses. Data from Bennett and Faulkes (2000) and Schneider and Kappeler (2014) respectively.

(a) Mole rats	Social organisation	Species	Number in burrow	Max litters per year
	Solitary	<i>Bathyergus suillus</i>	1	2
		<i>Bathyergus janetta</i>	1	2
		<i>Georchus capensis</i>	1	2
	Social	<i>Cryptomys h. hottentotus</i>	<14	2
		<i>Cryptomys amatus</i>	<25	3
		<i>Cryptomys darlingi</i>	<11	4
		<i>Cryptomys mechowii</i>	<8	3
		<i>Fukomys damarensis</i>	<41	4
		<i>Heterocephalus glaber</i>	<295	4
(b) Mongooses	Social organisation	Species	Number in group (mean; range)	Number of litters per year
	Solitary	<i>Atilax paludinosus</i>	-	2
		<i>Galeralla sanguinea</i>	-	2
		<i>Herpestes auropunctatus</i>	-	2-3
		<i>Herpestes edwardsii</i>	-	2-3
		<i>Herpestes javanicus</i>	-	2-3
		<i>Ichneumia albicauda</i>	-	1
	Social	<i>Crossarchus obscurus</i>	10-20	2.5
		<i>Cynictis penicillata</i>	~7-20	2
		<i>Helogale parvula</i>	9; 2-32	3
		<i>Herpestes ichneumon*</i>	1.7; 1-5	1.5
		<i>Mungos mungo</i>	24; 8-75	4
		<i>Suricata suricatta</i>	3-50	3-4

* Note that *H. ichneumon* show pronounced variability in social organisation (from solitary individuals to pairs and groups) and have previously been classified as both solitary and social.

Figure legends

Figure 1: (A) The cumulative work frequency of non-breeders increases with group size (points show the cumulative work frequency of all non-breeders in a group from each behavioural scan session). (B) The individual frequency of work decreases as group size rises, especially in breeding females. (C) The individual frequency of resting and eating increases as group size rises, and especially in breeding females. Lines in panels B,C show predictions from GLMMs, with associated 95% credible intervals (raw data points are shown in Figure S1).

Figure 2: Within groups, higher cumulative work by non-breeders over the final 45 days before parturition is associated with: (A) lower work frequency of the breeding female; (B) higher resting and eating frequency by the breeding female; (C) higher weight gain in the breeding female. Points are litter-level deviations from the population mean (best linear unbiased predictors [BLUPs] from multivariate GLMM, used for visualisation purposes only).

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Figure 3: (A) The inter-birth interval (number of days between a breeding female's consecutive litters) is shorter in larger groups. (B) Breeding females in larger groups are more likely to produce larger litters. (C) Breeding females in larger groups gain more weight over gestation than those in smaller groups. In all panels, points show raw data, lines are predicted from GLMMs (averaging

over any other covariates), and shaded grey areas indicate 95% credible intervals. In panel C, predictions are shown for 3 representative group sizes.

Figure 4: Cooperative behaviours may be maintained by either shared direct benefits ('mutualistic' cooperation) or indirect benefits to the fitness of relatives ('altruistic' cooperation). Images from top: Orca (*Orcinus orca*), L. Brent; ursine (red) howler monkey (*Alouatta arctoidea*), C. Crockett; house mice (*Mus musculus domesticus*), B. Boatman; Damaraland mole rat (*Fukomys damarensis*), P. Vullioud; dwarf mongoose (*Helogale parvula*), A. Morris-Drake; Kalahari meerkat (*Suricata suricatta*), T. Houslay.

Figure 1

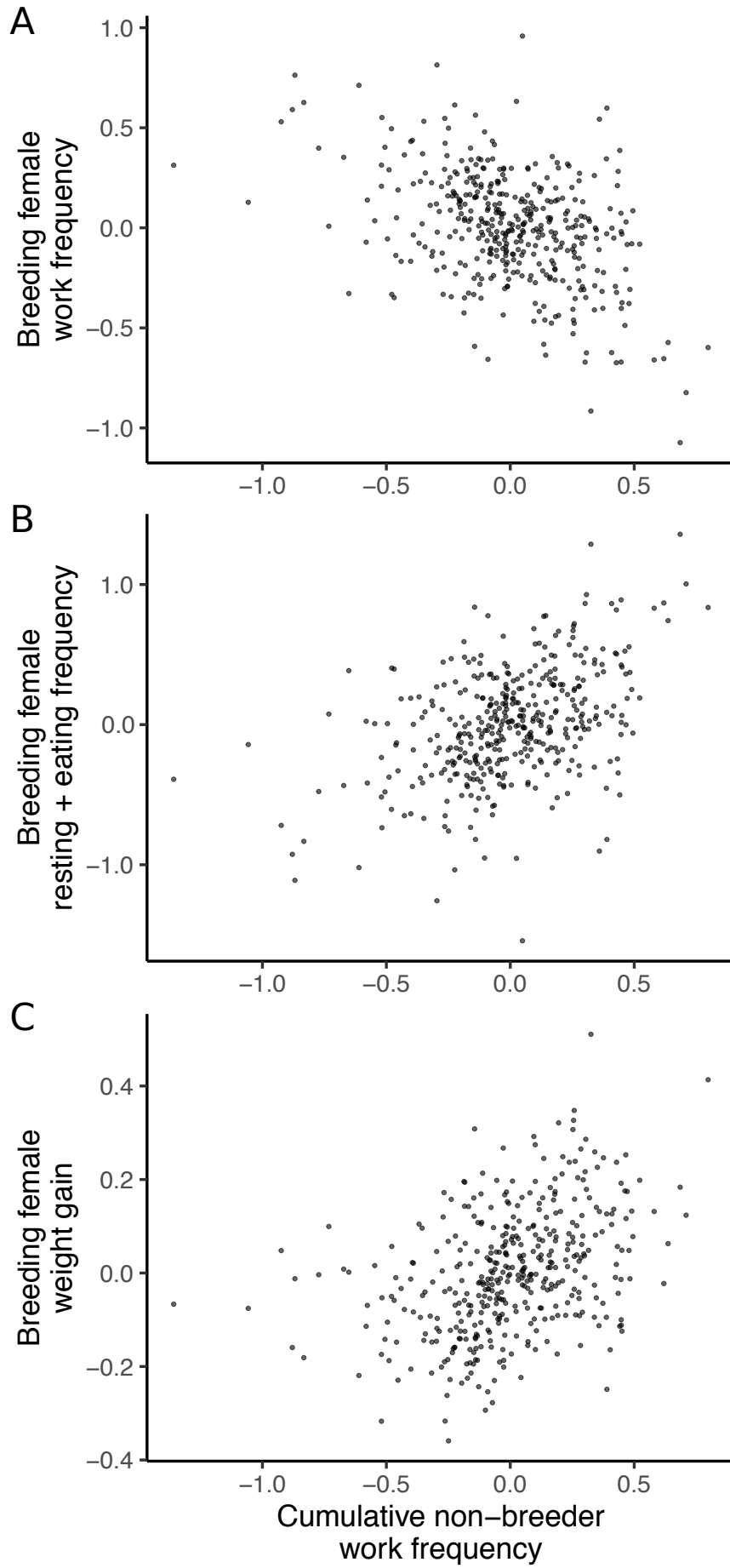


Figure 2

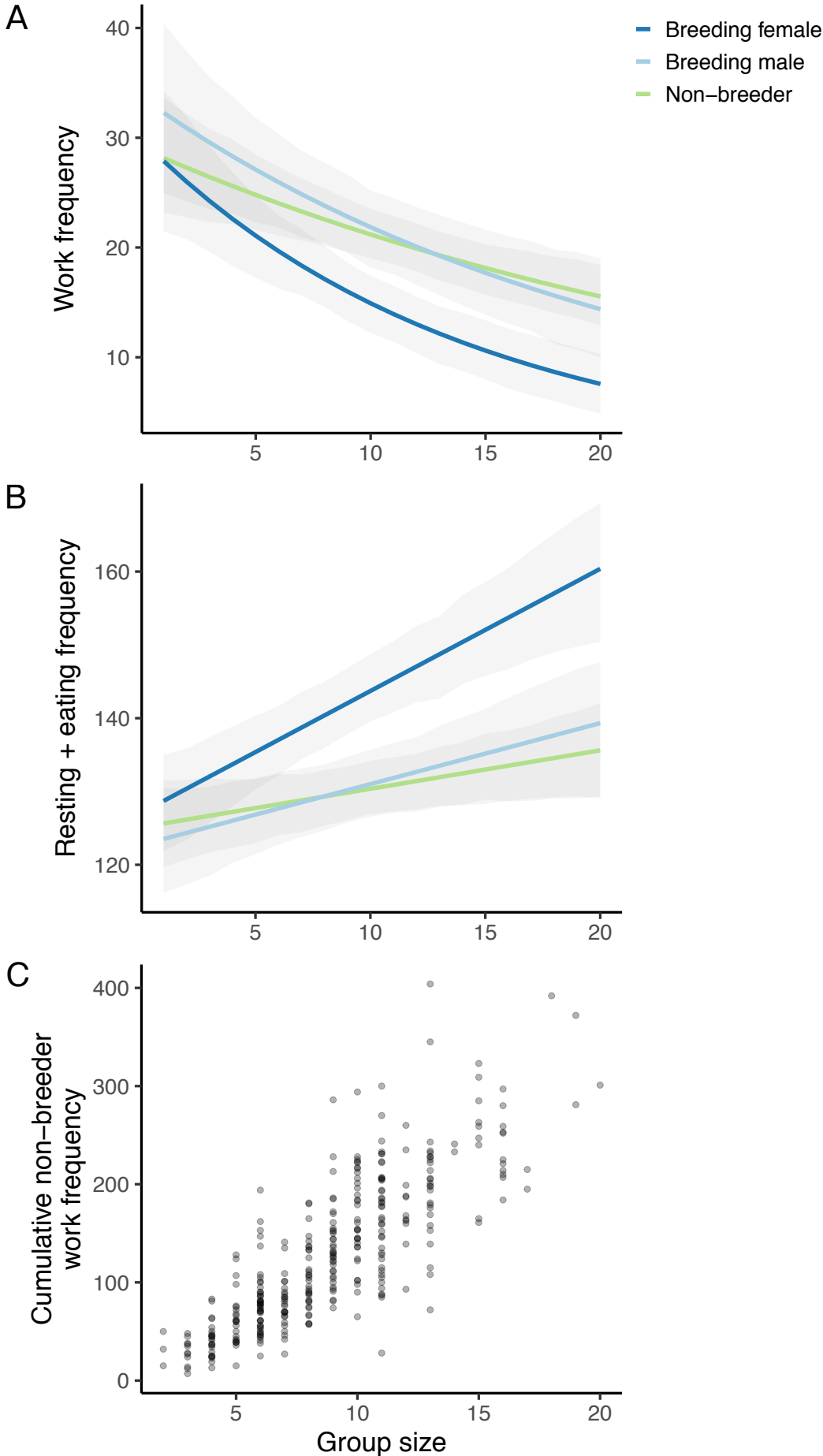


Figure 3

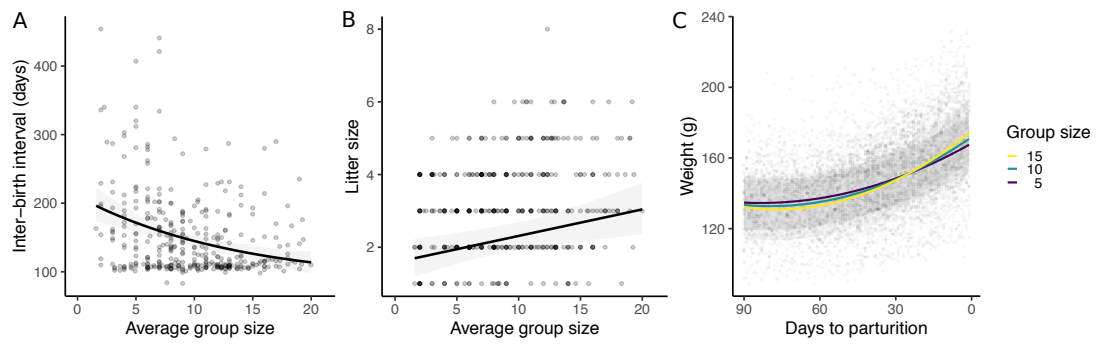


Figure 4

