Sex and age influence responses to changes in the cost of cooperative care in a social carnivore

Matthew B.V. Bell
Large Animal Research Group, Department of Zoology, University of Cambridge, Downing Street, Cambridge, CB2 3EJ, UK

In cooperative breeders, variation in contributions to offspring care will often be determined by variation in the cost of care. Because the cost of investment is determined by its effect on residual reproductive value, a unit of care should impose different fitness costs on different life-history categories of helper. This means that a change in current condition should have category-specific effects on contributions to care. I test this in the cooperatively breeding banded mongoose (*Mungos mungo*), experimentally increasing the cost of care by subjecting helpers to temporary deprivation. I observed category-specific effects on pup provisioning: For a given percentage weight loss, female helpers reduce their provisioning by a greater extent than male helpers. This is likely to be because variation in condition has a stronger effect on female reproductive success, so females should be under stronger selection to limit the cost of offspring care. I also observed an unexpected effect of age, with older helpers reducing their provisioning by more than younger helpers. This is probably because older helpers are more likely to breed themselves, so changes in condition may have a more immediate effect on direct fitness. In general, category-specific responses to changes in state should occur wherever there are existing category-specific differences in contributions to care, in both cooperative breeders and biparental species. *Key words:* banded mongoose, cooperative care, life-history trade-offs, parent–offspring conflict. *[Behav Ecol 21:1118–1123 (2010)]*

T here is considerable variation in contributions by helpers to offspring care in cooperatively breeding species (Cockburn 1998; Griffin and West 2003; Cant and Field 2001). In many cases, this variation can be explained by variation in relatedness (Reyer 1984; Komdeur 1994; Russell and Hatchwell 2001), although many species show limited sensitivity to relatedness (Brown 1987; Jacobs and Jarvis 1996; Cockburn 1998; Queller et al. 2000; Clutton-Brock et al. 2000, 2001). Such limited sensitivity may be a constraint imposed by sensory systems incapable of accurately detecting relatedness (Komdeur and Hatchwell 1999; Nakagawa and Waas 2004). It is also likely to be a result of variation in the cost of investing in someone else's offspring, which may often differ between helpers, even when they are equally related (or even unrelated) to the recipients of care (Heinsohn and Legge 1999; Clutton-Brock et al. 2000, 2002; Cant and Field 2001; Russell et al. 2003; Field et al. 2006).

The cost of investment in offspring is not strictly determined by absolute units of investment (mass of food provided, amount of energy expended, etc); it is determined by its effect on future capacity to reproduce (Trivers 1972; Kacelnik and Cuthill 1990). Therefore, the fitness cost of a unit of investment will usually depend on the life-history category of the carer, with carers in life-history categories whose residual reproductive value is more strongly affected by investment under stronger selection to limit the cost of investment (Cant and Field 2001; Field et al. 2006; Ward et al. 2009). One way to investigate this is to observe how carers in different life-history categories alter their investment after a change in condition. In general, reduced current condition should increase the cost of investment (Russell et al. 2003)—and the magnitude of the increase should be category specific. Therefore, the effect of a change in condition on levels of care should be category specific, with life history categories whose residual reproductive value is more affected by current investment reducing care by a greater extent in response to reduced condition.

Here, I investigate whether experimentally induced changes in state have category-specific effects on pup provisioning by helpers in banded mongooses (*Mungos mungo*). Banded mongooses are small (>2 kg) cooperatively breeding carnivores, where pups are cared for in exclusive associations with a single helper (termed an "escort," Cant 1998). Previous work indicates that there are sex-specific effects of variation in state on reproductive success (Hodge 2007; Hodge et al. 2009) and that this may influence patterns of care, with females generally providing less care than males (Hodge 2007). This implies that investment is more costly for females, so females may be more sensitive to changes in state than males. I tested this by temporarily removing escorts from their groups and depriving them of food for 1 day, expecting female escorts to reduce pup provisioning by a greater extent than males. An advantage of the banded mongoose escort system is that compensation by other adults is not an issue: Individual decisions about the trade-off between current and future investments are not influenced by the possibility of others compensating for any shortfall.

METHODS

Study site and data collection

Between May 2004 and August 2005, I conducted experiments on a wild population of banded mongooses in Queen Elizabeth National Park, Uganda (lat 0°12′S, long 27°54′E) (see Cant 2000 for habitat and climate details). All individuals were habituated to close (<5 m) observation on foot, and accurate ages (±2 days) were known for most of the population (92%). Individuals aged 0–3 months were classified as pups and >3 months as helpers (animals as young as 3 months have been observed provisioning pups, MBVB, personal observation). All

animals were tattooed for permanent identification, whereas for field identification, fully grown animals were fitted with color-coded plastic collars (weight 1.5 g, regularly checked to ensure a loose fit) (see Cant 2000 for trapping and marking procedures). Growing animals and some well-habituated animals were given unique haircuts.

All animals were trained to step on an electronic lab scale (accuracy ±1.5 g) before foraging in the morning (ca. 7:30). Animals were weighed again after foraging in the evening (ca. 18:30) and hourly weight change calculated as the change in weight (grams) divided by time between weighing sessions (hours).

Behavioral observations were carried out by the author and a field assistant, using handheld PSION II data loggers (model LZ-64), running purpose-written programmes where each individual in a pack and each target behavior were pre-allocated to a key combination, allowing observers to record rapid behavioral data without a break in observation.

This research was carried out under license from Uganda National Council for Science and Technology and all procedures approved by Uganda Wildlife Authority.

Study species

Banded mongooses live in large family groups (average number of adults = 29, range: 5–40) and are one of the few cooperative species where subordinates regularly breed (median number of breeding females per group = 4, range: 1–12). Packs usually breed 4 times each year, with all pregnant females usually giving birth simultaneously, producing large communal litters (median litter size = 5, range: 1–23). After birth, pups remain in dens for 3–4 weeks. When they emerge, they spend 3–5 days approaching different helpers, after which each pup forms an exclusive association with a single adult, with whom it spends ≥70% of its time and from whom it receives most of its food (median = 100%; Gilchrist 2004; Hodge 2005; Bell 2007). While foraging, pups follow escorts closely (usually within 10 cm), begging constantly. Associations remain stable until independence (ca. 9–13 weeks; Cant 1998; Gilchrist 2004).

The pup–escort relationship and escort feeding

To quantify associations between pups and helpers, we carried out 2 h of scan observations each day once new litters started foraging. Every 5 min, for each pup, we recorded distance to (± 10 cm) and identity of the nearest helper. At the end of each session, we classified a helper as an "escort" if the same pup was within 2 m for ≥40 % of scans. We defined a helper as a pup's "usual" escort after recording the same pup–helper pair on at least five consecutive observation sessions (average time between the first and last of the consecutive observation sessions = 5 days, range: 3–17).

When pup habituation allowed, we conducted focal watches on pups, following each pup for ≥20 min, recording ad libitum food items provided by helpers and found by pups themselves. At the end of every minute, we recorded the identity of every helper who was within 2 m of the pup for ≥20 s. For each focal watch, we calculated helper provisioning rate and pup self-feeding rate per minute observed.

Escort deprivation experiment

To investigate the effect of a change in state on escort provisioning rates, we conducted a series of escort deprivation experiments. On control mornings, we carried out focal watches on 23 escort–pup pairs as soon as their packs started foraging (ca. 07:45). The following morning, we removed the escorts as

they emerged from the den (ca. 07:30), releasing them after the pack had finished foraging in the evening (ca.18:30). On the morning following deprivation, we carried out a second set of focal watches on the same escort–pup pairs as soon as their packs started foraging. To control for any effect of disruption on packs as a whole, we carried out simultaneous focal watches on 22 unmanipulated escort–pup pairs, on both the control morning and the postdeprivation morning.

When capturing, we distracted the target animal with droplets of milk dispensed from a hamster water bottle, then grasped it by the scruff of the neck, and put it into a covered box trap (Tomahawk Live Trap Co., WI). In a few cases, target animals were too nervous to catch by hand, so we baited the trap and used a string release for the door. The morning after deprivation, we carried out repeat focal watches on the experimental pup–escort pairs as soon as their packs started foraging. To minimize any effects of pup age on behavior after escorts removal, we carried out removals within 20–25 days after pups first emerged (average age = 48 days, range: 44–53).

Ethical note

Escort removals took 5–10 minutes, and packs were not usually disturbed because adults seldom gave distress calls when trapped. We kept removed animals in their traps, which were large enough to allow free movement (trap dimensions = 66 × 23 × 23 cm; average banded mongoose body length = 52 cm). We covered the traps with a blanket and stored them on the floor of a cool shed with access to water but no food. Removed animals spent an average of 10.5 h out of the group (±0.1 standard error [SE]). Escorts were accepted back with minimal aggression (usually subjected to anal marking by dominant animals) and pup–escort associations never broke down as a result of experimental manipulation (MBVB, unpublished data).

Adult banded mongooses are frequently separated from their packs for up to 11 h—they remain behind in the den as babysitters (Cant 2003). This means that the period of deprivation experienced by these animals was well within the natural range. However, removing animals and keeping them in traps are clearly likely to be considerably more stressful. To minimize this stress, we 1) captured animals in pairs because a companion seemed to reduce distress; 2) placed traps in a cool darkened shed, covered by a blanket, because darkness calmed the animals, and they usually spent most of the removal period asleep; 3) provided an ad lib source of water from a hamster water bottle; 4) checked animals at least once an hour to monitor for signs of distress or injury; and 5) ensured that the shed in which they were stored was left undisturbed and was secure from ants, predators, and toxins. Removal had no discernible effect on behavior after release—animals showed no increase in wariness toward observers and allowed themselves to handled and weighed as before removal. In many cases, animals would voluntarily reenter a trap within minutes of release in search of food, indicating that they had not formed a negative association with the trap.

Clearly, removal of an escort will have consequences for dependent pups. These were explored in detail (Bell 2008), with no evidence for lasting negative effects.

Statistical analysis

To determine whether there were category-specific effects on the change in provisioning after deprivation, I constructed a general linear mixed model (LMM) with percentage change in provisioning rate as the response variable and percentage body weight lost by the escort, escort age, and escort sex as

explanatory variables (see Table 1 for all potential explanatory variables tested). I included random terms for Litter and Pack to account for repeated sampling (Schall 1991), with the variance components estimated using the restricted maximum likelihood method. Analysis was conducted on 21 escorts with 21 different pups (9 female escorts with 5 male and 4 female pups and 12 male escorts with 7 male and 5 female pups) from 10 litters in 4 packs (2 pup–escort pairs excluded because behavioral observations were disrupted by rain or elephants). Because the response variable is percentage change, it is not bound at 0 and 100 (the range is between -100 and $+80$), which means that the data were normally distributed (confirmed by a Kolmogorov–Smirnov (KS) test = 0.144, $P > 0.15$). During analysis, residuals from the model were visually inspected to ensure homogeneity of variance, normality of error, and linearity. A KS test confirmed that the residuals were normally distributed (KS = 0.12, $P > 0.15$).

During model selection, I sequentially dropped all potential explanatory terms from the full model, starting with the least significant term in the full model and continuing until only terms whose elimination would have significantly reduced the explanatory power of the model remained. Once the minimal model had been established, each dropped term was added back into the minimal model in turn to obtain their level of nonsignificance and to verify that significant terms had not been incorrectly excluded (after Crawley 2002). Repeating the analysis by successive inclusion of significant terms to build a minimal model de novo yielded an identical final model. I tested all 2-way interactions but only present those explaining significant variation. I present the effect sizes of all significant terms—these are parameter estimates from the models and can be interpreted as the change in y per unit change in x. For categorical variables, such as sex, one level of the factor is set at 0, and the effect is relative to that factor level.

Simple parametric tests were conducted in Minitab (all tests 2-tailed), and linear models constructed using Genstat 8.1 (Lawes Agricultural Trust, Rothamsted, Harpenden, UK).

RESULTS

Escort weight loss

Escorts lost an average of 48.4 g (± 4.01 SE) during removal (an average of $-3.4\% \pm 0.22$ SE of body weight). This is in comparison with an average gain of 49.4 g (± 5.4 SE) across a similar time period on unmanipulated days (an average of $+3.5\% \pm 0.4$ SE of body weight). There were no sex-specific differences in percentage weight loss (average percentage weight lost: females = 3.08 ± 0.28 SE, males = 3.49 ± 0.30 SE; 2 sample t-test, $t = 1.0$, $P = 0.33$) and no relationship between age and percentage weight loss (linear regression, $F_{1,19} = 0.20$, $P = 0.66$). There was no difference in pup begging rate (average begging rate: control morning = 41.0 begs per min ± 2.68 SE, postdeprivation morning = 42.1 begs per minute ± 3.20 SE; paired t-test, $t = 0.52$, $P = 0.61$), indicating that any changes in escort provisioning were not the result of changes in pup demand.

Escort provisioning rates

Following deprivation, experimental escorts reduced their provisioning rate whereas control escorts continued to provision at similar rates (2-way repeated measures analysis of variance [ANOVA], interaction between escort treatment [deprived or control], and experimental stage [before or after deprivation]: $F_{1,41} = 8.51$, $P = 0.006$; Figure 1).

There were sex-specific effects of deprivation on escort provisioning: Female escorts were more sensitive to weight loss than males, reducing their provisioning rate by more than male escorts for the same percentage weight loss (LMM, interaction between percentage body weight lost and escort sex: $\chi^2_{1,20} = 4.96$, $P = 0.026$; Table 1; Figure 2a). There was also an effect of escort age, with older escorts showing larger reductions in provisioning rate ($\chi^2_{1,20} = 6.95$, $P = 0.008$; Table 1; Figure 2b).

The reduction in provisioning rate allowed deprived escorts to gain weight more rapidly than before deprivation, with females gaining more weight than males (2-way repeated measures ANOVA, interaction between sex and experimental stage [before or after deprivation]: $F_{1,41} = 4.67$, $P = 0.04$; Figure 3). This indicates that reduced provisioning is an
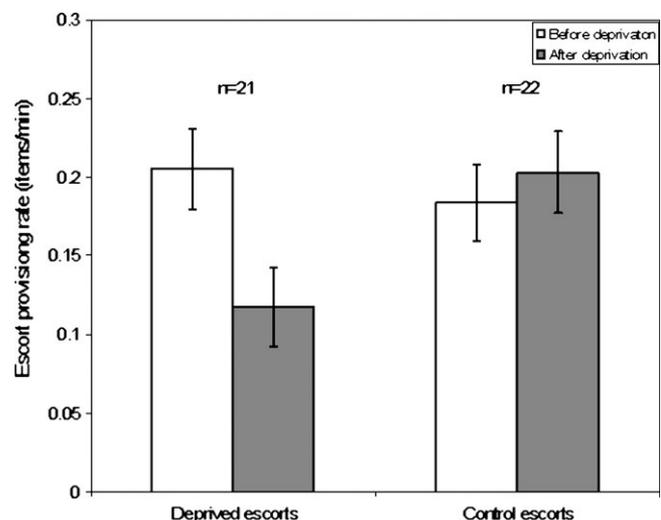
Table 1

General linear mixed model of variables affecting the percentage change in escort provisioning rate after experimental deprivation (analysis was conducted on 21 escorts with 21 pups)

Explanatory terms	Wald statistic (χ^2) (degrees of freedom = 1, 20)	P
Escort age (days)	6.95	0.008
Escort % weight loss	5.41	0.02
Escort sex (M)	0.51	0.47
Escort % weight change $\times$ escort sex	4.96	0.026
Pup weight	0.45	0.50
Pup age	0.07	0.79
Pup sex	0.01	0.91

Minimal model	Effect size	SE
Constant	0.49	0.24
Escort age (days)	-0.00035	0.00013
Escort % weight loss	-3.18	1.36
Escort sex (M)	0.15	0.22
Escort % weight change $\times$ escort sex	55.87	25.08

Random term	Estimated variance	SE
Group	0.016	0.057
Litter	0.0026	0.069

Figure 1
Deprived and control escort provisioning rate before and after experimental escorts had undergone a day of experimental deprivation (means $\pm$ SE).
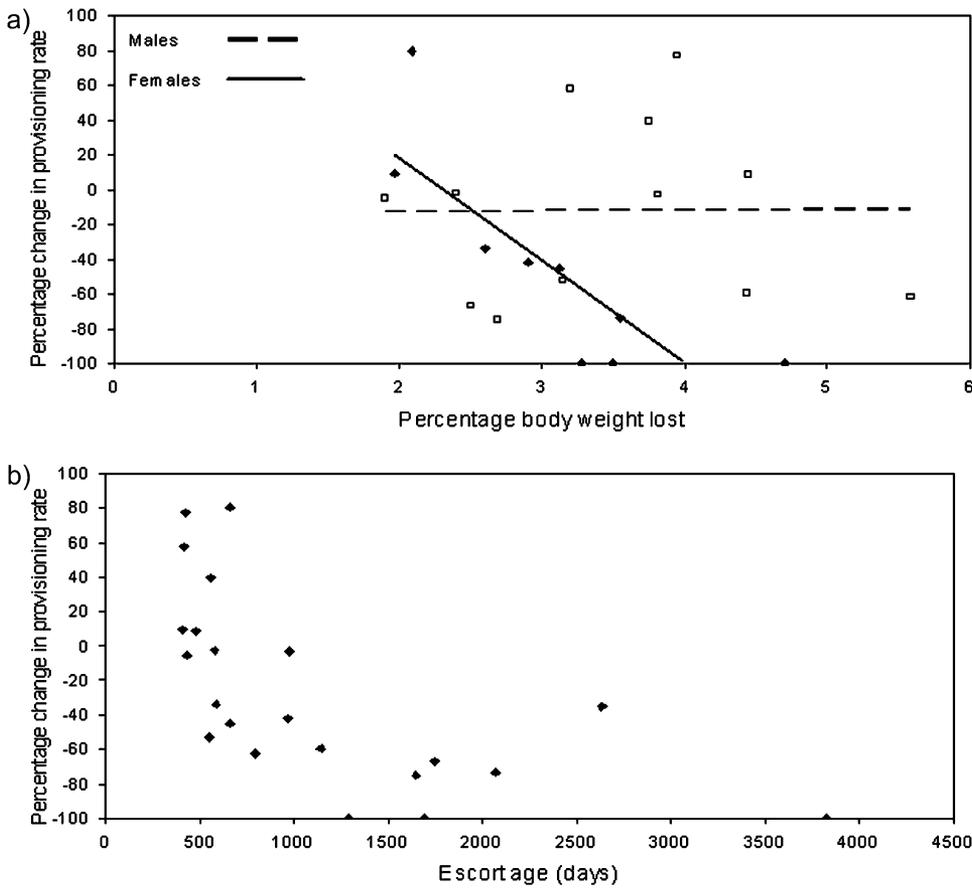
Figure 2
Changes in deprived escort provisioning rate after experimental deprivation: (a) the interaction between percentage weight loss and escort sex and (b) the effect of escort age. Points are raw data; lines are linear regressions fitted through the data.

adaptive reaction to deprivation rather than a by-product of disrupted foraging or stress related to the removal and reflects the greater sensitivity of females to deprivation.

DISCUSSION

The cost of offspring investment should depend on its effect on the residual reproductive value of the carer—which will itself depend on the life-history category of the carer (Cant and Field 2001; Russell et al. 2003). This means that there should be category-specific effects of a change in state on provisioning by helpers in cooperative breeders. The results presented here confirm this: There is a sex-specific effect of weight loss on provisioning, with female escorts being more sensitive to

weight loss than male escorts. There is also an effect of age, with older escorts being more sensitive to deprivation than younger escorts.

Females are probably more responsive to weight loss because changes in condition have a greater effect on female reproductive success (Hodge 2007; Hodge et al. 2009). In particular, the escorting period usually coincides with conception and gestation of the subsequent litter, with lighter females much less likely to conceive or carry to term (Gilchrist et al. 2004). Moreover, pup weight is strongly influenced by maternal weight at conception (Hodge et al. 2009), and pup weight in turn has profound consequences for pup competitive ability, growth, survival, and age at first reproduction (Hodge 2005; Hodge et al. 2009). By contrast, male reproductive
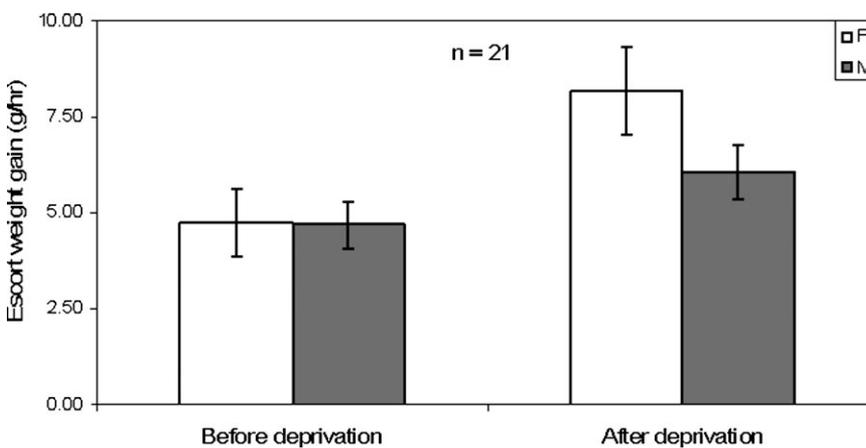

Figure 3
Experimental escort hourly weight gain before and after experimental deprivation (means ± SE).

success appears to be more governed by age rank rather than by weight (Hodge 2003; Nichols et al. 2010), and males are generally able to regain weight lost as a result of escorting before competing in the next breeding attempt (Hodge 2007). The results presented here in fact mirror previous provisioning experiments, which demonstrated that male escorts increased their provisioning rates after supplementary feeding, but female escorts did not (Hodge 2007).

In general, we should expect the sex whose reproductive success is more influenced by changes in condition to show greater sensitivity to a change in state and to show greater variation in contributions to care. For instance, where there are sex differences in dispersal, the dispersing sex often invests less in cooperative care (Brotherton et al. 2001; Clutton-Brock et al. 2002), possibly in compensation for the cost of dispersal. That sex is likely to be more sensitive to changes in state, reducing contributions more dramatically during periods of shortage. We might therefore expect the dispersing sex to show more extreme seasonal variation in contributions to care.

The effect of age on provisioning was unexpected: Care is usually expected to be more costly for younger individuals (Heinsohn and Cockburn 1994) because they are still investing in growth (Brotherton et al. 2001; Clutton-Brock et al. 2001) or because their foraging skills are not yet fully developed (Heinsohn 1991; Thornton 2008). However, in banded mongooses, older individuals are more likely to breed themselves (Cant 2000; Hodge 2007; Nichols et al. 2010), and reduced current condition may have a more immediate effect on their direct fitness, whereas younger individuals may have ample time to regain condition before attempting to breed themselves (Russell et al. 2003; Hodge 2007).

Effects of life-history category on contributions to both cooperative and biparental care are common (Cockburn 1998; Clutton-Brock et al. 2002; Ward et al. 2009; Sumner et al. 2010) and should be expected wherever there are category-specific effects of investment on residual reproductive value. This study is unusual in that it demonstrates a category-specific response to deterioration in state, though the results mirror previous experiments demonstrating category-specific responses to supplementary feeding (e.g., Eden 1987; Boland et al. 1997; Clutton-Brock et al. 2002; Canestrari et al. 2007, 2008). Such category-specific responses to changes in state should occur wherever there are existing category-specific differences in contributions to care, in both cooperative breeders and biparental species. This has implications for our understanding of how individuals should respond to variation in contributions by collaborators or partners.

Individuals are generally expected to adjust their own contributions in response to changes by collaborators (Houston and Davies 1985; McNamara et al. 1999; Johnstone and Hinde 2006). Experimental manipulations of the cost of care are frequently conducted to investigate individual responses to changes in investment by collaborators (for reviews, see Hinde 2006 and Harrison et al. 2009). The majority of this work assumes that the fitness cost of a unit of care is the same for both partners and is constant across a breeding attempt. In fact, equal costs are very unlikely, and existing sex differences in care or desertion rate indicate underlying differences in the fitness cost of a unit of care—and should predict sex-specific responses to both changes in the cost of care and to changes in partner contributions. This may in part explain much of the variation in the results of handicapping experiments (Hinde 2006; Harrison et al. 2009). For instance, the timing of the experiments may strongly influence the outcome: If carried out early in the breeding season, male residual reproductive value may be higher than later in the breeding season, so males handicapped early should be more

sensitive to increased costs than those handicapped later. Male responses to female handicapping should also vary: Early in a breeding season, when male residual reproductive value is high, increased contribution will cost more per unit than later in the breeding season, so males may be less responsive to changes in female provisioning early in the breeding season.

The logic can be extended to any cooperative behavior where current investment has different effects on the residual reproductive value of the collaborators. Individuals will generally be selected to compensate for changes in investment by collaborators, but a unit of compensation will impose different fitness costs on different categories of collaborator. Predicting the outcome of these interactions will not be straightforward because it requires an understanding of the trade-off of current against future fitness for each collaborator.

REFERENCES

Bell MBV. 2007. Cooperative begging in banded mongoose pups. Curr Biol. 17:717–721.

Bell MBV. 2008. Receiver identity modifies begging intensity independent of need in banded mongoose (*Mungos mungo*) pups. Behav Ecol. 19:1087–1094.

Boland CRJ, Heinsohn R, Cockburn A. 1997. Experimental manipulation of brood reduction and parental care in cooperatively breeding white winged choughs. J Anim Ecol. 66:683–691.

Brotherton PNM, Clutton-Broxk TH, O'Riain MJ, Gaynor D, Sharpe L, Kansky R, McIlrath M. 2001. Offspring food allocation by parents and helpers in a cooperative mammal. Behav Ecol. 12:590–599.

Brown JL. 1987. Helping and breeding in birds. Princeton (NJ): Princeton University Press.

Canestrari D, Chiarati E, Marcos JM, Ekman J, Baglione V. 2008. Helpers but not breeders adjust provisioning effort to year round territory resource availability in carrion crows. Anim Behav. 76:943–949.

Canestrari D, Marcos JM, Baglione V. 2007. Costs of chick provisioning in cooperatively breeding carrion crows: an experimental study. Anim Behav. 73:349–357.

Cant MA. 1998. Communal breeding in banded mongooses and the theory of reproductive skew. [PhD thesis]. Cambridge (UK): University of Cambridge.

Cant MA. 2000. Social control of reproduction in banded mongooses. Anim Behav. 59:147–158.

Cant MA. 2003. Patterns of helping effort in cooperatively breeding banded mongooses (*Mungos mungo*). J Zool. 259:115–121.

Cant MA, Field J. 2001. Helping effort and fitness in cooperative animal societies. Proc R Soc Lond B Biol Sci. 268:1959–1964.

Clutton-Brock TH, Brotherton PNM, O'Riain MJ, Griffin AS, Gaynor D, Kansky R, Sharpe L, McIlrath GM. 2001. Contributions to cooperative rearing in meerkats. Anim Behav. 61:705–710.

Clutton-Brock TH, Brotherton PNM, O'Riain MJ, Griffin AS, Gaynor D, Sharpe L, Kansky R, Manser MB, McIlrath GM. 2000. Individual contributions to babysitting in a cooperative mongoose, Suricata suricatta. Proc R Soc Lond B Biol Sci. 267:301–305.

Clutton-Brock TH, Russell AF, Sharpe LL, Young AJ, Balmforth Z, McIlrath GM. 2002. Evolution and development of sex differences in cooperative behaviour in meerkats. Science. 297:253–256.

Cockburn A. 1998. Evolution of helping behaviour in cooperatively breeding birds. Annu Rev Ecol Syst. 29:141–177.

Crawley MJ. 2002. Statistical computing. Chichester (UK): Wiley.

Eden ST. 1987. When do helpers help? Food availability and helping in the moorhen, *Gallinula chloropus*. Behav Ecol Sociobiol. 21:191–195.

Field J, Cronin A, Bridge C. 2006. Future fitness and helping in social queues. Nature. 441:214–217.

Gilchrist JS. 2004. Pup escorting in the communally breeding banded mongoose. Behav Ecol. 15:952–960.

Gilchrist JS, Otali E, Mwanguhya F. 2004. Why breed communally? Factors affecting fecundity in a communal breeding mammal: the banded mongoose (*Mungos mungo*. Behav Ecol Sociobiol. 57:119–131.

Griffin AS, West SA. 2003. Kin discrimination and the benefit of helping in cooperatively breeding vertebrates. Science. 302:634–636.

Harrison F, Barta Z, Cuthill I, Szekely T. 2009. How is sexual conflict over parental care resolved? A meta-analysis. J Evol Biol. 22: 1800–1812.

Heinsohn R, Cockburn A. 1994. Helping is costly to young birds in cooperatively breeding white-winged choughs. Proc R Soc Lond B Biol Sci. 256:293–298.

Heinsohn R, Legge S. 1999. The cost of helping. Trends Ecol Evol. 14:53–57.

Heinsohn RG. 1991. Slow learning of foraging skills and extended parental care in cooperatively breeding white winged choughs. Am Nat. 137:864–881.

Hinde CA. 2006. Negotiation over offspring care? A positive response to partner provisioning rate in great tits. Behav Ecol. 17:6–12.

Hodge SJ. 2003. The evolution of cooperation in the communal breeding banded mongoose. [PhD thesis]. Cambridge (UK): University of Cambridge.

Hodge SJ. 2005. Helpers benefit offspring in both the short and long term in the cooperatively breeding banded mongoose. Proc R Soc Lond B Biol Sci. 272:2479–2484.

Hodge SJ. 2007. Counting the cost: the evolution of male biased care in the cooperatively breeding banded mongoose. Anim Behav. 74: 911–919.

Hodge SJ, Bell MBV, Mwanguhya F, Kyabulima S, Waldick RC. 2009. Maternal weight, offspring competitive ability and the evolution of communal breeding. Behav Ecol. 20:729–735.

Houston DJ, Davies NB. 1985. The evolution of cooperation and life history in the dunnock (*Prunella modularis*). In: Sibly RM, Smith RH, editors. British ecological society, vol. 25. Behavoural ecology: ecological consequences of adaptive behaviour. Palo Alto (CA): Blackwell Scientific Publications. p. 471–487.

Jacobs DS, Jarvis JUM. 1996. No evidence for the work-conflict hypothesis in the eusocial naked mole-rat (*Heterocephalus glaber*). Behav Ecol Sociobiol. 39:401–409.

Johnstone RA, Hinde CA. 2006. Negotiation over offspring care–how should parents respond to each others efforts? Behav Ecol. 17: 818–827.

Kacelnik A, Cuthill I. 1990. Central place foraging in starlings (*Sturnus vulgaris*). 2. Food allocation to chicks. J Anim Ecol. 59: 655–674.

Komdeur J. 1994. The effect of kinship on helping in the cooperatively breeding Seychelles warbler (*Acrocephalus sechellensis*). Proc R Soc Lond B Biol Sci. 256:47–52.

Komdeur J, Hatchwell BJ. 1999. Kin recognition: function and mechanism in avian societies. Trend Ecol Evol. 14:237–241.

McNamara JM, Gasson CE, Houston AI. 1999. Incorporating rules for responding into evolutionary games. Nature. 401:368–371.

Nakagawa S, Waas JR. 2004. O sibling where art thou? A review of avian sibling recognition with respect to the mammalian literature. Biol Rev. 79:101–119.

Nichols HJ, Amos W, Bell MBV, Cant MA, Hodge SJ. Forthcoming 2010. Top males gain high reproductive success by guarding more successful females in a cooperative mongoose. Anim Behav.

Queller DC, Zacchi F, Cervo R, Turillazzi S, Henshaw MT, Santorelli LA, Strassmann JE. 2000. Unrelated helpers in a social insect. Nature. 405:784–787.

Reyer HU. 1984. Investment and relatedness: a cost/benefit analysis of breeding and helping in the pied kingfisher *Ceryle rudis*. Anim Behav. 32:1163–1178.

Russell AF, Hatchwell BJ. 2001. Experimental evidence for kin-biased helping in a cooperatively breeding vertebrate. Proc R Soc Lond B Biol Sci. 268:2169–2174.

Russell AF, Sharpe LL, Brotherton PNM, Clutton-Brock TH. 2003. Cost minimisation by helpers in cooperative vertebrates. PNAS. 100:3333–3338.

Schall R. 1991. Estimation in generalised linear models with random effects. Biometrika. 78:719–727.

Sumner S, Kelstrup H, Fanelli D. 2010. Reproductive constraints, direct fitness and indirect fitness benefits explain helping behaviour in the primitively eusocial wasp, *Polistes candensis*. Proc R Soc Lond B Biol Sci. 277:1721–1728.

Thornton A. 2008. Variation in contributions to teaching by meerkats. Proc R Soc Lond B Biol Sci. 275:1745–1751.

Trivers RL. 1972. Parental investment and sexual selection. In: Campbell B, editor. Sexual selection and the descent of man. Chicago (IL): Aldine. p. 1871–1971.

Ward RJS, Cotter SC, Kilner RM. 2009. Current brood size and residual reproductive value predict offspring desertion in the burying beetle *Nicrophorus vespilloides*. Behav Ecol. 20:1274–1281.