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Alloparental behaviour and long-term costs of mothers tolerating other group-members in a plurally breeding mammal

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Cooperative-breeding studies tend to focus on a few alloparental behaviours in highly cooperative species exhibiting high reproductive-skew, and the associated short-term, but less frequently long-term, fitness costs. We analyse a suite of alloparental behaviours (assessed via filming) in a kin-structured, high-density population of plurally breeding European badgers *Meles meles* that are not highly cooperative. Group members, other than mothers, performed alloparental behaviour; however, this was not correlated with their relatedness to within-group young. Furthermore, mothers babysat, allogroomed cubs without reciprocation, and allomarked cubs more than other group-members (controlling for observation time). For welfare reasons we could not individually mark cubs, however, the number observed pre-independence never exceeded that trapped. All 24 trapped cubs, in three filmed groups, were assigned both parents using 22 microsatellites. Mothers may breed cooperatively as the time they babysat the equivalent or more than their assigned litter size did not differ. Furthermore, two mothers probably allonursed as they suckled more cubs than their assigned litter size. An 18-year genetic pedigree, however, detected no short-term (litter size; maternal survival to the following year) or long-term (offspring breeding probability; offspring lifetime breeding success) fitness benefits with more within-group mothers or other group-members. Rather, the number of other group-members correlated negatively with long-term fitness. Mothers may tolerate other group-members as non-breeders undertook more digging. Our study highlights that alloparental care varies on a continuum from that seen in this high-density badger population, where alloparenting behaviour is minimal, through to species where alloparental care is common and provides fitness benefits.

Keywords: communal breeding; cooperative breeding; plural breeding; alloparental care; helpers; allonursing; *Meles meles*; CERVUS; microsatellite; lifetime reproductive success

Cooperative breeding refers to social systems in which group members that are not the (assumed) genetic parents care for offspring (Brown 1987; Solomon & French 1997). Studies of cooperative breeding have been largely restricted to groups with high reproductive-skew (i.e. a low proportion of females breed), with fewer examples from societies that are not highly cooperative, and from plurally breeding societies (Macdonald et al. 1987; Pusey & Packer 1994; Lewis & Pusey 1997; Gilchrist 2006). Alloparental care occurs when breeding individuals care for non-offspring in plurally breeding groups, or when non-breeders care for offspring, and may be sex-biased (Cockburn 1998). As individuals are selected to maximise their own fitness, why individuals provide alloparental care rather than focusing on their own reproduction is a central question in evolutionary biology. Alloparents may gain indirect fitness benefits (Hamilton 1964) and direct benefits such as breeding experience, increased future probability of breeding, or enhanced survival (summarised in: Riedman 1982; Jennions & Macdonald 1994; König 1997; Solomon & French 1997; Cockburn 1998).

Functional benefits to cooperative breeding have been inferred in some species through correlations of reproductive success with the number of alloparents (Jennions & Macdonald 1994; Cockburn 1998; Solomon & Crist 2008). These correlations, however, can be confounded by factors such as territory quality (Woodroffe & Macdonald 2000). Other species show no relationship between the number of alloparents and group reproductive success (Cockburn 1998; Macdonald et al. 2004; Ebensperger et al. 2007), but this does not necessarily mean that alloparents do not increase group productivity, especially if alloparents gain long-term fitness advantages (Hatchwell et al. 2004; Hodge 2005; Russell et al. 2007a).

Benefits of alloparental care have, however, been demonstrated experimentally through removal of alloparents (Komdeur 1994), removal of offspring (Clutton-Brock et al. 2001), or cross-fostering (Russell et al. 2007b), and have been suggested by statistical elucidation of between-individual and within-individual effects in combination with pair-wise comparisons (Cockburn et al. 2008).

In this study we investigate the contribution of group members to a suite of alloparental behaviours in a high-density population of the European badger *Meles meles*. This is a promising species in which to investigate the evolution of social behaviours as its social organisation varies, from solitary to pair- and group-living, across its geographic range (Johnson et al. 2000). In high-density populations in southern England, badgers live in groups, that tend to form in woodlands surrounded by farmland, and breed once a year around February (Woodroffe & Macdonald 1995). They have a polygynandrous mating system; plural breeding occurs within social groups, approximately 50% of the cubs are sired by extra-group males, and the mean litter size is 1.3–1.5 (Carpenter et al. 2005; Dugdale et al. 2007). Cubs are born underground, where they usually remain for their first eight weeks, and independence occurs by 15 weeks (Neal & Cheeseman 1996). Dispersal is restricted (Pope et al. 2006) and groups are maintained by natal philopatry of both sexes (Macdonald et al. 2008). Within-group adults and yearlings are related (average $R = 0.2$) by less than assigned half-siblings ($R = 0.3$), but more than unrelated individuals ($R = 0.0$, Dugdale et al. 2008). Low levels of positive reproductive skew occur in both sexes (i.e. slightly fewer individuals breed than random expectation), and skew in females is likely to be controlled by individual adaptation to local food availability and reproductive suppression through female–female aggression (Dugdale et al. 2008; Dugdale et al. 2010). Cooperative breeding has been suggested by Woodroffe (1993) who observed three female badgers at one sett for ten hours: two non-breeding females groomed cubs and babysat when the assumed mother was not present. A second study suggested that cubs in two social groups spent more time with assumed breeding-females than other group-members (Fell et al. 2006). Further observations are required, over longer periods, and at several groups, along with genetic parentage assignments and statistical techniques that allow for repeated measures, which our study provided.

Throughout this paper we use the term alloparent rather than helper, to avoid fitness implications (Solomon & French 1997; Gilchrist 2007). Additionally, we use the term cooperative rather than communal breeding. Communal breeding implies shared parentage and use of a communal nest or den (Solomon & French 1997); however, in badgers it is unknown as to whether non-breeders alloparent, and cubs may be raised in more than one sett (den) or nest chamber within a social group (Roper 1992).

We examine which group members perform alloparental behaviours in six social-group-years (three independent groups). Cooperative behaviours are those performed by an individual that benefit others and are selected, at least in part, due to this benefit (West et al. 2007). We examine seven potential cooperative behaviours: five are direct interactions with offspring (babysitting, cub carrying, allogrooming, allomarking and non-offspring suckling, Jennions & Macdonald 1994; Pusey & Packer 1994; König 1997; Koenig & Dickinson 2004), and two are indirect interactions (digging and bedding collection, Solomon 1991; Powell & Fried 1992).

Babysitters remain at the sett to guard cubs, from foxes or intruding badgers, while other group-members leave the sett to forage (Woodroffe 1993). Cub carrying occurs when group members carry cubs over-ground between sett entrances (Woodroffe 1993), potentially to change nest chambers and reduce ectoparasite loads (Roper et al. 2001). Allogrooming may be reciprocated or unreciprocated in a tit-for-tat strategy, however, cubs rarely reciprocate allogrooming before ten weeks of age (Stewart 1997). Allogrooming is a behaviour through which ectoparasites may be removed, particularly from regions that badgers cannot reach themselves (Stewart 1997; Macdonald et al. 2000). Sequential allomarking occurs when the actor lifts its tail and presses its anal region onto the body of the receiver (Buesching et al. 2003). This marks the receiver with sub-caudal gland secretion (primary social odour source), which contains group-specific odours (Buesching et al. 2002). Cubs do not produce this secretion until 4–6 months of age, hence cubs need to be marked so that their group membership can be recognised (Buesching 2000). Suckling is rarely seen above ground in badgers (Woodroffe 1993; Neal & Cheeseman 1996). Allosuckling may provide non-offspring with nutrients, however, allosuckling may be both adaptive and non-adaptive (Hayes 2000). Finally, sett maintenance behaviours (digging, and bedding [e.g. grass, leaves, bracken] collection) peak around the cub-rearing period (Neal & Cheeseman 1996). Sett maintenance behaviours may benefit all group-members but in particular they may improve cub survival by reducing female–female competition for limited breeding sites (Stewart et al. 1999), providing thermoregulatory assistance (Neal & Cheeseman 1996) and reducing ectoparasite loads (Cox et al. 1999).

We recorded the identity of individuals performing these five direct and two potential indirect alloparental behaviours and used 22 microsatellite loci to assign parentage and assess relatedness. We then asked whether: 1) group members perform direct alloparental behaviour; 2) breeding females provide alloparental care to more young than they are assigned parentage to; 3) group members vary their alloparental care according to their relatedness to group young; and, 4) individuals differ in their contribution to potential indirect alloparental behaviours. Furthermore, we use an 18-year genetic pedigree to examine whether, 5) alloparental behaviour is related to fitness benefits in the short-term (increased litter size or probability of maternal survival to the next year), or long-term (increased probability of offspring breeding, or increased offspring lifetime breeding success).

METHODS

We filmed two neighbouring groups from 1st February to 31st May, in 1995, 2004 and 2005 in Wytham Woods, Oxfordshire (01° 19’W, 51° 46’N). The primarily deciduous woodlands are enclosed by a deer fence containing most of the badger setts (dens) and encompassing 4 km^2. The highest density was 44.3 badgers km^{-2}, between 1987 and 1996 (Macdonald & Newman 2002). Based on trapping records (1987–2005), badgers were present in 14–26 social groups each year (mean = 19 [17, 21]). Means are provided with the lower and upper 95% confidence interval limits, respectively. There were a mean of 5.6 [5.2, 6.0] (range = 1–23) candidate mothers and 5.8 [5.4, 6.2] (range = 1–26) candidate fathers per social-group-year, and up to seven mothers and seven fathers were assigned parentage within a social-group-year (mean = 1.9 [1.8, 2.0] for both sexes), with 80% confidence (Dugdale et al. 2007). Social groups consist of a main sett and several smaller setts throughout the territory, however, trapping records do not enable inference of which sett a female bred at and cubs may be moved between setts within a territory.

Fieldwork was conducted under English Nature Licence 20001537 and Home Office Licence PPL-30/1216. Trapping events generally took place four times a year, for one week in January, and for two weeks in each of June, August and November (Macdonald & Newman 2002). Badgers were trapped, sedated and identified using methods detailed elsewhere (Dugdale et al. 2003; Hewitt et al. 2009). Briefly, badgers were caught in box traps baited with peanuts, which were set at dusk and checked, then closed, at dawn. Badgers were sedated with 0.2 ml ketamine hydrochloride (Vetlar; Pharmacia and Upjohns, Crawley, U.K.) per kg bodyweight (Thornton et al. 2005). Guard hair (*ca* 100) and blood (*ca* 3 ml from the jugular vein) samples were collected for genetic analyses. We used ultrasound methodologies

(Woodroffe 1995), and a 45-day gestation period (Dumartin et al. 1989) to estimate the mean birth date in the filmed groups, each year. Woodroffe (1995) generated a regression equation of foetus length as a predictor of age using raw data in Dumartin et al. (1989). Applying this regression to the extrapolated minimum and maximum foetus lengths in Dumartin et al. (1989) over the first trimester (when ultrasound is undertaken) suggests an accuracy range of -2.6–3.2 days (mean = 0.3 [-0.3, 0.9]). Two of the six social-group-years had ultrasound data from more than one pregnant female, and the mean number of days between estimated birth dates within the same social-group-year was 4.0 [0.3, 7.7] (range = 0–10, $N = 6$).

Genetic Analyses

Badgers were genotyped for 16–22 microsatellite loci (using blood or guard-hair samples), parentage was assigned with 80% and 95% confidence, and kinship and relatedness were estimated using methods described previously (Dugdale et al. 2007; Dugdale et al. 2008). Briefly, parentage was assigned using CERVUS 3.0.1.8 (Kalinowski et al. 2007) and sibships were reconstructed using COLONY 1.2 (Wang 2004). Average relatedness (*R*) was estimated using RELATEDNESS 5.0.8 (Queller & Goodnight 1989). Parentage was only assigned for cubs trapped after independence; the rate of pre-emergence mortality is unknown. We assigned both parents to all 24 cubs in the filmed groups, and we assigned both parents to 595 (94%) of the 630 cubs born 1988–2005, with 80% confidence, or 331 (53%) cubs with 95% confidence (Dugdale et al. 2007). We assessed whether breeding females could confidently be assigned as full-siblings or mother–offspring rather than unrelated using KINSHIP 1.3.1 (Goodnight & Queller 1999).

Behavioural Analyses

Behavioural observations were made using infrared-sensitive remote video surveillance (Stewart et al. 1997) at one social group in three years, a second social group in two years and a third group in one year (i.e. six social-group-years; table 1). Data were collected continuously, throughout the night, around active sett entrances (Stewart et al. 1999). Cameras were placed *ca* three meters up a tree and covered a field-of-view of *ca* 13m^2. Filming equipment was installed and checked during daylight hours to minimise disturbance to the nocturnal badgers. The field-of-view covered activity areas (trampled ground where badger social behaviour takes place) to minimise the chance of missing behaviours. We analysed 11 230 h of footage (960 videotapes or 319 calendar nights). Adults and yearlings were individually identified through fur clip-marks (Stewart & Macdonald 1997). Cubs could not be trapped and clip marked until week 15, which is after independence; therefore, cubs were not individually identifiable. Inter-observer reliability is provided in the electronic supplementary information, and the composition of each social-group-year in table 1. Unmarked badgers, and occasionally unidentifiable marked badgers, were recorded in separate categories, recording the maximum number of unmarked / unidentifiable individuals observed at any one time.

Behaviours were recorded either per incidence or per bout of activity. Bouts of activity commenced when the first badger appeared on screen and ended with ≥ 60 s without a badger on screen. We also recorded the duration of time that cubs spent on their own (‘cub record’, 128 h) and with other non-cub group-members (‘cub and group-member record’, 75 h), along with the maximum number of cubs in the field-of-view. If all group-members left the field-of-view and the cubs followed within 5 s, a separate ‘cub record’ was not made. Records were continued if cubs went off screen and returned within 10 s. We behaviourally analysed footage from up to three weeks before birth and then up to and including week 17 post-birth. Six cooperative behaviours were recorded:

1. *Babysitting*: records were classified as ‘cub and group-member record’ in which a group member (whose identity was recorded) interacted with the cub, the group member moved to within at least one cub body-length of the cub and the cub did not retreat from them (70 h). Fifty-eight percent of this time (41 h) cubs were with one group-member, 20% (14 h) with two, and 22% (15 h) with 3–9 group-members. We excluded the latter records, to remove events when non-babysitting group-members were not away from the sett foraging; however, these data provided qualitatively similar results (supplementary table 1 & supplementary Fig.1*a*&*b*), in terms of which group-members babysat, as the restricted datasets. The total time that each individual babysat was summed over each week of the cubs’ lives, with week one being the first week of life. If an individual was seen on screen with cubs in a given week, but did not babysit, then we entered their babysitting time as zero; however, if they were not seen on screen with cubs no babysitting record was entered. Babysitting data were statistically analysed from week seven to 13, inclusive, as cubs do not generally emerge until week eight and lactation lasts 12 weeks, with cub independence by week 15 (Neal & Cheeseman 1996).
2. *Cub carrying*: group members usually carry cubs by grasping the scruff of the cub in their mouth (Woodroffe 1993). The identity of the actor was recorded and a separate record made for each incidence. Each incidence of cub carrying ended when the actor left the field-of-view with the cub, the actor and cub went into the sett, or the cub was left in the field-of-view and was not carried again by the actor in the same bout of badger activity.
3. *Unreciprocated allogrooming:* we recorded when a group member allogroomed a cub, without the cub reciprocating the allogrooming, once per ‘cub and group-member record’.

The identity of the actor was noted.

4. *Sequential allomarking*: we recorded each time a cub was sequentially allomarked, along with the identity of the actor.
5. *Suckling*: we identified suckling if the cub's head was positioned at a nipple and, if a microphone was used, suckling was heard. Suckling females were generally laid on their back or side, or occasionally they were on their feet, in which case the cub's head was twisted upwards. A bout of suckling ended when the female moved away or when there was no suckling for at least 20 s. The identity of the female, the maximum number of cubs that suckled, and the total duration of the suckling bout were recorded.
6. *Sett maintenance*: the number of digging records were recorded such that each record finished when the actor stopped digging and moved away, or moved back into the sett entrance to start another digging record. One bedding collection record was made each time an actor took bedding into a sett.

Statistical Analyses

Statistical analyses were conducted using SAS 9.2 (Littell et al. 2006). We ran General and Generalised Linear Mixed Models (GLMMs) using the MIXED procedure for normally distributed responses and the GLIMMIX procedure with Poisson, negative binomial (NBD) or binomial error (BED) distributions. Parameters were estimated using restricted maximum likelihood (MIXED procedure) and Laplace approximation (GLIMMIX procedure). Denominator degrees of freedom were estimated using the Kenward-Roger method in the MIXED procedure and the containment method in the GLIMMIX procedure (Littell et al. 2006). Continuous fixed effects were Z-score standardised (Gelman & Hill 2007).

We analysed the absolute and relative, number or duration, of events within a social-group-year. Relative contributions differ from absolute contributions as they take into account behaviours performed by unmarked group-members. Absolute numbers of events were fitted with a Poisson error distribution and log link in the GLIMMIX procedure, except where we specify a NBD error distribution with log link (selected using Akaike's Information Criteria [AIC]). Absolute durations of events were analysed in the MIXED procedure and were log transformed, first adding a constant to move the minimum value to one when necessary (Osborne 2002). Relative contributions were analysed in the GLIMMIX procedure with BED and logit link. In BED models the number of times or length of time that identifiable individuals performed an event was fitted as the numerator, and the total number of events or duration observed in that social-group-year was fitted as the denominator, including events by unmarked or unknown badgers. Behaviours were analysed per week, except for rare events (cub carrying and suckling), and behaviours that showed no time-trend pattern (sett maintenance). These were summed per social-group-year.

Badger identity, or badger identity nested within a social group (each badger was only observed in one group) when analysing weekly occurrences, was included as a random effect. Random effects were removed when their variance estimates were zero. Social group was fitted as a fixed categorical effect, as three levels are not enough to adequately estimate variance through inclusion as a random effect. Badgers were categorised according to their sex and breeding status (breeding male or female, or non-breeding male or female), where breeder indicates parentage of that year's within-group cubs. Unmarked or unidentifiable badgers were excluded from these categories, as repeated measures on the same unmarked individual could not be controlled for.

Fixed fields-of-view are problematic as some badgers may be rarely seen, although they are close by, hence, there is a greater chance of observing cooperative breeding behaviours by those individuals that are on screen for longer. Similarly, the rate at which individuals perform alloparental behaviours may vary. We therefore included the number of times that each individual was seen on screen (sett maintenance analyses), or seen on screen with cubs (other analyses) plus the amount of footage recorded (per time-period within a social-group-year), along with the number of non-cub group-members within a social-group-year (group size), and the number of cubs within each social-group-year as covariates in all analyses. Social group was also included as a categorical fixed effect, as detailed above. Further statistical details, specific to each analysis, are detailed in the electronic supplementary material.

RESULTS

Do Group Members Perform Direct Alloparental Care?

Although other group-members did babysit, breeding females babysat more than other group-members each week in both absolute and relative terms (Fig.1*a*&*b*, supplementary table 2; supplementary Fig.2*a*&*b*, supplementary table 3). There was an interaction between badger category and the age of the cubs in the relative but not in the absolute analyses (supplementary tables 2 & 3), such that mothers babysat less and other group-members babysat more as the cubs became older, but only in the relative analysis which incorporates behaviours of unmarked individuals in the denominator (Fig.1 and supplementary Fig.2).

We observed 186 cub-carrying events by both males and females (weeks 4–16); 72% were by breeding females. Males performed 10% of the 186 cub-carrying events, usually during play, and the first observation was at week 10. Cub carrying by males was distinct from that by females, seen from week four, whereby cubs were generally carried in and out of sett entrances. Breeding females carried cubs more than other group-members (including non-breeding females) in absolute terms, but not in relative terms (table 2). Relative analyses include contributions by unmarked individuals, including an unmarked breeding female in 2005 (table 1), which influenced this result.

Breeding females allogroomed cubs without reciprocation (supplementary table 4 & Fig.2*a*&*b*) and sequentially allomarked cubs (supplementary table 5 & Fig.3*a*&*b*) more than other group-members in both the absolute and relative models. The relative proportion of both behaviours increased for other group-members and decreased for mothers over the weeks (Figs. 2*b* & 3*b*), as did the absolute number of sequential allomarking events of cubs (Fig.3*a*), but not the absolute number of unreciprocated allogrooming events of cubs (Fig.2*a*).

Do Breeding Females Care for More Young than they are Assigned Parentage to?

The total time when a breeding female was the only babysitter, and when the maximum number of cubs equalled their litter size or less (mean = 74 [42, 106] minutes), was not different significantly to the time they spent babysitting when the maximum number of cubs on screen was greater than their litter size (mean = 40 [20, 60] minutes; $S_{10} = 21$, $P = 0.067$). Although the p-value was low, these data suggest that breeding females may care for more young than they were assigned maternity of.

We observed 23 occurrences of suckling, all by breeding females in April 2004 (weeks 8–10) and April 2005 (weeks 9–13). Suckling lasted a mean of 1.6 [1.1, 2.1] minutes (all 23 records), or 1.1 [0.5, 1.7] minutes (taking the mean duration of suckling per mother, $N = 5$). Two females suckled more cubs then their assigned litter size, which we refer to as potential allonursing. One female suckled 2–4 cubs, on four occasions, but had a litter size of one; she had negative LOD (the log-likelihood ratio of the likelihood of that female being the mother relative to the likelihood of a random female) scores for four of the other cubs within the social-group-year and a low positive score for the remaining cub. Five other females in the group had a higher LOD score for this cub. This female terminated three of the suckling bouts, which could indicate discrimination of the female against non-offspring; however, the cubs terminated one suckling bout. This female had three foetuses at ultrasound on 15/01/2005, but reabosrption of embryos may have later occurred (Yamaguchi et al. 2006). A second female suckled three cubs once, for two minutes, when her litter size was two; she had negative LOD scores for all of the other four cubs within that social-group-year. This female terminated the suckling while there was one cub left suckling. Ultrasound data were not available for this female.

Do Individuals Vary their Alloparental Care According to their Relatedness to Group Young?

Excluding breeding females, neither absolute nor relative babysitting levels with one babysitter were related to badger category or average relatedness to within-group cubs (table 3). Similar results were seen with up to two babysitters (supplementary table 6).

Five filmed social-group-years contained more than one breeding female, and three of these contained mothers that were all more likely to be full-siblings, or equivalent, than unrelated individuals (table 4). Potential allonursing events were observed in one of these groups (P 2005).

Do Individuals Differ in their Contribution to Potential Indirect Alloparental Behaviours?

Badgers did not differ in their contributions to bedding collection (supplementary table 7; Fig.4*a*&*b*). Breeders contributed the least to digging (Fig.4*c*&*d*) in both the absolute and relative models (supplementary table 8).

Do Alloparents Gain Short-term or Long-term Fitness Benefits?

Using an 18-year genetic pedigree (1988–2005), neither litter size nor the probability of a mother surviving to the next year were related to either the number of within-group mothers or other group-members when analysing social-group-years in which all cubs were assigned a mother or in which at least one mother was assigned (table 5).

Male cubs had a greater probability of breeding in their lifetime than females (males = 0.42 [0.37, 0.49], females = 0.27 [0.21, 0.33] in social-group-years in which at least one cub was assigned a mother; males = 0.43 [0.35, 0.51], females = 0.29 [0.22, 0.37] in groups in which all cubs were assigned a mother; table 6). The number of mothers in a cub's group was not related to the probability of a cub breeding or the lifetime breeding success of a cub (table 6). The number of other group-members within a social-group-year, however, had a negative relationship with both the probability of a cub breeding and the lifetime breeding success of a cub (table 6).

DISCUSSION

Breeding females babysat more throughout the cub-rearing period, and also sequentially allomarked and allogroomed cubs without reciprocation more than other group-members did, controlling for the number of times individuals were seen on screen with cubs. Although other group-members performed cub-rearing behaviours, the combined duration and frequency of this represented a small proportion of the group total and may simply represent social integration of the cubs into the group (i.e. an increase in social interactions with non-parent group members). Mothers decreased and other group-members increased their alloparental behaviour over time in terms of their relative and absolute sequential allomarking, and their relative (but not absolute) babysitting and unreciprocated allogrooming behaviours. Additionally, the babysitting contribution of other group-members did not differ according to their category or their average relatedness to the within-group cubs.

Overall, breeding females performed the majority of the cub-rearing behaviours, and may have provided alloparental care to non-offspring. When there was only one babysitter, the total time that breeding females babysat their assigned litter size, or less, did not differ from the time they spent babysitting more cubs than their assigned litter size. Furthermore, although observations of suckling were rare, two breeding females potentially allonursed; however, suckling durations were short and observation of suckling does not necessarily imply milk transfer, nor that it is adaptive (Hayes 2000). Future studies are required to estimate the prevalence of this behaviour.

We could not confirm whether breeding females provided alloparental care to non-offspring because cubs were not individually identifiable. The maximum number of cubs observed on screen was greater than the maximum number trapped only once out of the 11 230 h analysed (at week 13, i.e. cub independence, so this was potentially a neighbouring cub). Overall, it is therefore unlikely that cubs surviving to emergence died before they were trapped at independence.

Alloparental behaviour may be an unselected, stimulus driven response to the presence of young (Jamieson & Craig 1987); however, this is more likely to explain how alloparental behaviour first arose than account for its persistence in many mammalian populations (Emlen et al. 1991). Breeding females may not be able to differentiate between own and non-offspring via their primary social odour source, sub-caudal gland secretion, as cubs do not produce this until 4–6 months of age (Buesching 2000). Therefore, if cubs from more than one female's litter are kept in the same nest chamber (unknown in badgers) this may hinder females detecting their own offspring, as suggested in degu *Octodon degus*

(Ebensperger et al. 2007). Consequently, we hypothesise that late onset of odour secretion may be a strategy for cubs to induce alloparental care. Future behavioural observations of visually marked offspring while still underground will improve our understanding of badger breeding behaviour. In particular, as allonursing is potentially costly, investigations into its frequency in badgers, and factors that affect the likelihood of allonursing, such as litter size, relatedness to non-offspring and presence of own offspring (Pusey & Packer 1994), are required.

A previous study investigated the social integration of cubs into two badger groups and concluded that cubs spent most of the cub-rearing period with assumed breeding females than other age / sex classes (Fell et al. 2006). Fell *et al*. (2006), however, were not able to benefit from the advantages afforded our study by: parentage data, large and independent data sets, use of GLMMs that control for random and repeated measures, and observations of suckling. Our study is therefore the first to identify that female badgers, of assigned breeding status, may rear young cooperatively. Further studies of marked and genotyped cubs are required to confirm the extent of alloparental behaviours in badgers, especially in lower density populations as our study population has one of the highest reported densities, and behaviours are likely to vary with density (Frantz et al. 2010).

Do alloparents gain short-term or long-term fitness benefits?

To classify alloparental care as helping, it must have some measurable benefit. Woodroffe (1993) reported that non-breeding females babysat; however, this did not constitute helping as the increase in group productivity of yearlings with the number of non-breeding females was an artefact of territory quality (Woodroffe & Macdonald 2000). Our study indicates that breeding females rather than other group-members rear cubs, and that this may include non-offspring. There was no relationship however, between litter size and the number of within-group mothers, when territory quality and year were controlled. Other studies (Macdonald et al. 2004; Ebensperger et al. 2007) have also shown no relationships between the number of alloparents and short-term measures of reproductive success. Long-term effects have been statistically inferred, such as the age at which offspring first breed (Hodge 2005), and experimentally established, such as the likelihood of offspring obtaining breeding status (Russell et al. 2007a).

There was no relationship between the number of mothers in a badger cub's natal group, at birth, and offspring lifetime breeding success or probability of offspring breeding. It is possible that we did not have power to detect this. As the mean lifespan of badgers with an early age of last breeding (< 9 years) is 4.8 years [4.3, 5.3], and that of badgers with a late age of last breeding (> 8 years) is 9.7 years [8.6, 10.8] (Dugdale *et al.* 2010), an 18-year genetic pedigree (containing 422 estimates of lifetime breeding success) should have power to investigate this relationship. There may be other undetected benefits, however. For example, alloparenting may increase the survival of breeding females (reviewed in Jennions & Macdonald 1994); however, we detected no effect of the number of mothers on the probability of mothers surviving to the following year. Alternatively, alloparenting may affect maternal weight which influences maternal fecundity (Russell et al. 2003). Body condition affects implantation date (Woodroffe 1995; Dugdale et al. 2003) and whether female badgers breed in years of poor resource availability (Woodroffe & Macdonald 1995). By sharing babysitting duties, breeding females may increase their foraging time thereby increasing the resources that they can provide to offspring; however, as badgers forage away from the sett this study was not able to measure foraging time.

Within-group relatedness is high in badger groups (Dugdale et al. 2008) and breeding females in three of the five social-group-years that contained more than one mother were more likely to all be first order relatives than unrelated. Breeding females may therefore gain indirect fitness benefits through alloparental care of their sister's cubs, which may not be costly to provide given that they all already are caring for their own offspring; however, no measureable benefits were detected.

Group members, other than mothers, did perform some babysitting, but this was not related to their average relatedness to within-group young. The number of other group-members (excluding mothers) was not associated with short-term (maternal litter size or maternal survival probability) fitness benefits. In the long-term male cubs had a greater probability of breeding than females, as due to delayed implantation males may sire cubs in the year after their death. Controlling for this, an increase in the number of group members (other than mothers) in the cub's natal group at birth, decreased the probability of cubs breeding and decreased the lifetime reproductive success of cubs.

Why Allow Non-breeders and Other Mothers to Remain in the Group?

Reproductive skew within badger social groups is likely to result from resource availability and incomplete reproductive suppression (Dugdale et al. 2008). Linear dominance hierarchies were found in three out of the six social-group-years analysed in this study, with breeding females ranking highest (Hewitt et al. 2009); however, whether breeding females can control group membership is unknown. As there were no detectable costs or benefits to an increased number of mothers in a group, mothers may tolerate other mothers within their group.

Other group-members (excluding mothers) may be tolerated by mothers, as although there were long-term costs to an increased number of other group-members (excluding mothers), other group-members do contribute to alloparental care (albeit minimally) and non-breeders contribute to sett maintenance – again there may be undetected benefits to this behaviour. Non-breeding individuals may also be tolerated within the group because territorial boundary marking is partitioned between group members (Kilshaw et al. 2009). Furthermore, non-breeding individuals performed more digging during the cub-rearing season and all group-members contributed to bedding collection. Stewart *et al.* (1999) found that digging was more common in large, frequently copulating males, whereas we found that breeding males (i.e. those that successfully mated the previous year) dig less than non-breeding males. We did not observe a sex-bias in digging, but this may be an artefact of our shorter study period, over the post-partum mating period which may affect digging behaviour.

We have demonstrated that breeding females performed the majority of the cub-rearing behaviours and potentially provided alloparental care. Further studies are required to establish the extent of such behaviours. Alloparenting may have low-costs to breeding females compared to non-breeding females that may better spend their time acquiring resources to improve their likelihood of breeding next year. High values of relatedness between female group-members may provide indirect benefits to cooperative cub-rearing behaviours by breeding females; however no short- or long-term benefits were detected. Long-term costs of increased numbers of other group-members (excluding mothers) were detected, but not short-term costs. Mothers may tolerate the other group-members as we show that other group-members contribute minimally to alloparental behaviours and to a larger extent to sett maintenance.

It is only through the development of a large number of microsatellite markers that we were able to discriminate between first-order relatives of the offspring and the true parents, while not knowing either maternity or paternity *a priori*. This, in tandem with behavioural analyses, enabled detection of alloparental behaviour in a high-density badger population. Alloparental care varies on a continuum from that seen in badgers and some felids

(Macdonald et al. 1987; Pusey & Packer 1994) where alloparenting behaviour is minimal, through to some canids (Macdonald et al. 2004) and mongooses (Russell et al. 2007a) where alloparental care is commonly observed and linked to fitness benefits. Studies in lower-density group-living populations are required to evaluate the extent of alloparental care and the fitness consequences of group living, to provide a better understanding of whether increased population density pushes group-living species along the sociality scale.

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FIGURE LEGENDS

Figure 1. Mean (a) absolute number of minutes per week, and (b) relative proportion of time per week (incorporating unmarked/unidentifiable individuals), that group members were observed as the only babysitter, against cub age in weeks. Group members were classified as breeding females (♀–B) or other group-members. Error bars display ± one standard error (SE). The figures display the mean predicted values from GLMMs, which controlled for repeated measures of individuals nested within a social group as a random effect and the following fixed effects: the number of times an individual was seen on screen with cubs, observation time, group size, the number of cubs in the group and social-group identity. Model estimates ± SE for the intercept, week, category (other group-member) and week x category were: (a) absolute model: 1.70 ± 0.13, -0.14 ± 0.09, -0.86 ± 0.14, 0.23 ± 0.12; and, (b) relative model: -1.43 ± 0.28, -0.39 ± 0.04, -2.62 ± 0.27, 0.90 ± 0.10, respectively (see supplementary table 2 for the complete model estimates).

Figure 2. Mean (a) absolute number, and (b) relative proportion, of ‘cub and group-member records’ in which group members allogroomed cubs without reciprocation, against cub age in weeks. Group members were classified as breeding females (♀–B) or other group-members. Error bars display ± one standard error. The figures display the mean predicted values from GLMMs, which controlled for repeated measures of individuals nested within a social group as a random effect and the following fixed effects: the number of times an individual was seen on screen with cubs, observation time, group size, the number of cubs in the group and social-group identity. Model estimates ± SE for the intercept, week, category (other group-member) and week x category were: (a) absolute model: 1.33 ± 0.14, 0.11 ± 0.05, -1.14 ±

0.16, 0.17 ± 0.11; and, (b) relative model: -1.62 ± 0.19, -0.44 ± 0.06, -1.64 ± 0.21, 0.52 ± 0.12, respectively (see supplementary table 4 for the complete model estimates).

Figure 3. Mean (a) absolute number, and (b) relative proportion, of times that group members allomarked cubs, against cub age in weeks. Group members were classified as breeding females (♀–B) or other group-members. Error bars display ± one standard error. The figures display the mean predicted values from GLMMs, which controlled for repeated measures of individuals nested within a social group as a random effect and the following fixed effects: the number of times an individual was seen on screen with cubs, observation time, group size, the number of cubs in the group and social-group identity. Model estimates ± SE for the intercept, week, category (other group-member) and week x category were: (a) absolute model: 0.86 ± 0.23, -0.22 ± 0.06, -1.04 ± 0.27, 0.60 ± 0.14; and, (b) relative model: -1.75 ± 0.29, -0.54 ± 0.07, -1.43 ± 0.32, 0.77 ± 0.16, respectively (see supplementary table 5 for the complete model estimates).

Figure 4. Mean number of times a badger in each category was observed: collecting bedding in (a) absolute and (b) relative terms; and, digging in (c) absolute and (d) relative terms. Relative analyses incorporate behaviour by unmarked/unidentifiable individuals in the denominator. Error bars display ± one standard error. Data labels represent the number of data points on which the means were obtained; seven females and three males were present in two years. B = breeder; NB = non-breeder. The figures display the mean predicted values from GLMMs, which controlled for repeated measures of individuals as a random effect and the following fixed effects: the number of times an individual was seen on screen, group size,

the number of cubs in the social-group-year, and social group identity. Bedding collection model estimates ± SE for the intercept (i.e. ♀–B) and category (♀–NB, ♂–B, ♂–NB) were: (a) absolute model: 1.81 ± 0.35, 0.23 ± 0.20, 0.05 ± 0.77, -0.38 ± 0.45; and, (b) relative model: -4.03 ± 0.36, 0.26 ± 0.21, 0.03 ± 0.79, -0.40 ± 0.46, respectively (see supplementary table 7 for the complete model estimates). Digging model estimates ± SE for the intercept (i.e. ♀–B) and category (♀–NB, ♂–B, ♂–NB) were: (a) absolute model: -0.37 ± 0.57, 4.32 ± 0.67, 3.43 ± 1.03, 4.59 ± 0.65; and, (b) relative model: -7.40 ± 0.73, 2.52 ± 0.48, 2.36 ± 1.52, 4.29 ± 0.92, respectively (see supplementary table 8 for the complete model estimates).

Figure 1

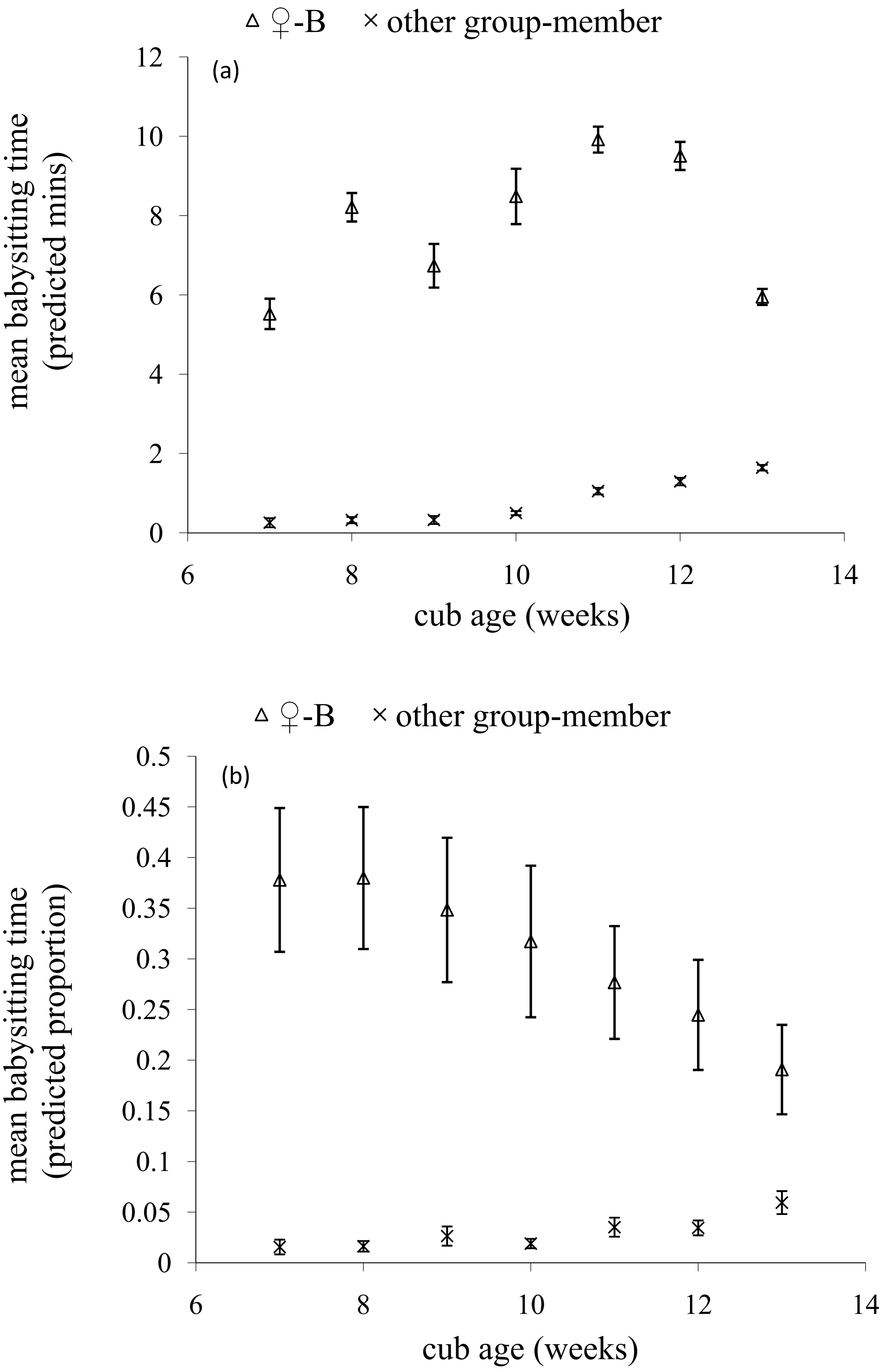
△ ♀-B × other group-member
(a)
mean babysitting time (predicted mins)
0
2
4
6
8
10
12
cub age (weeks)
6
8
10
12
14
△ ♀-B × other group-member
(b)
mean babysitting time (predicted proportion)
0
0.05
0.1
0.15
0.2
0.25
0.3
0.35
0.4
0.45
0.5
cub age (weeks)
6
8
10
12
14

Figure 2

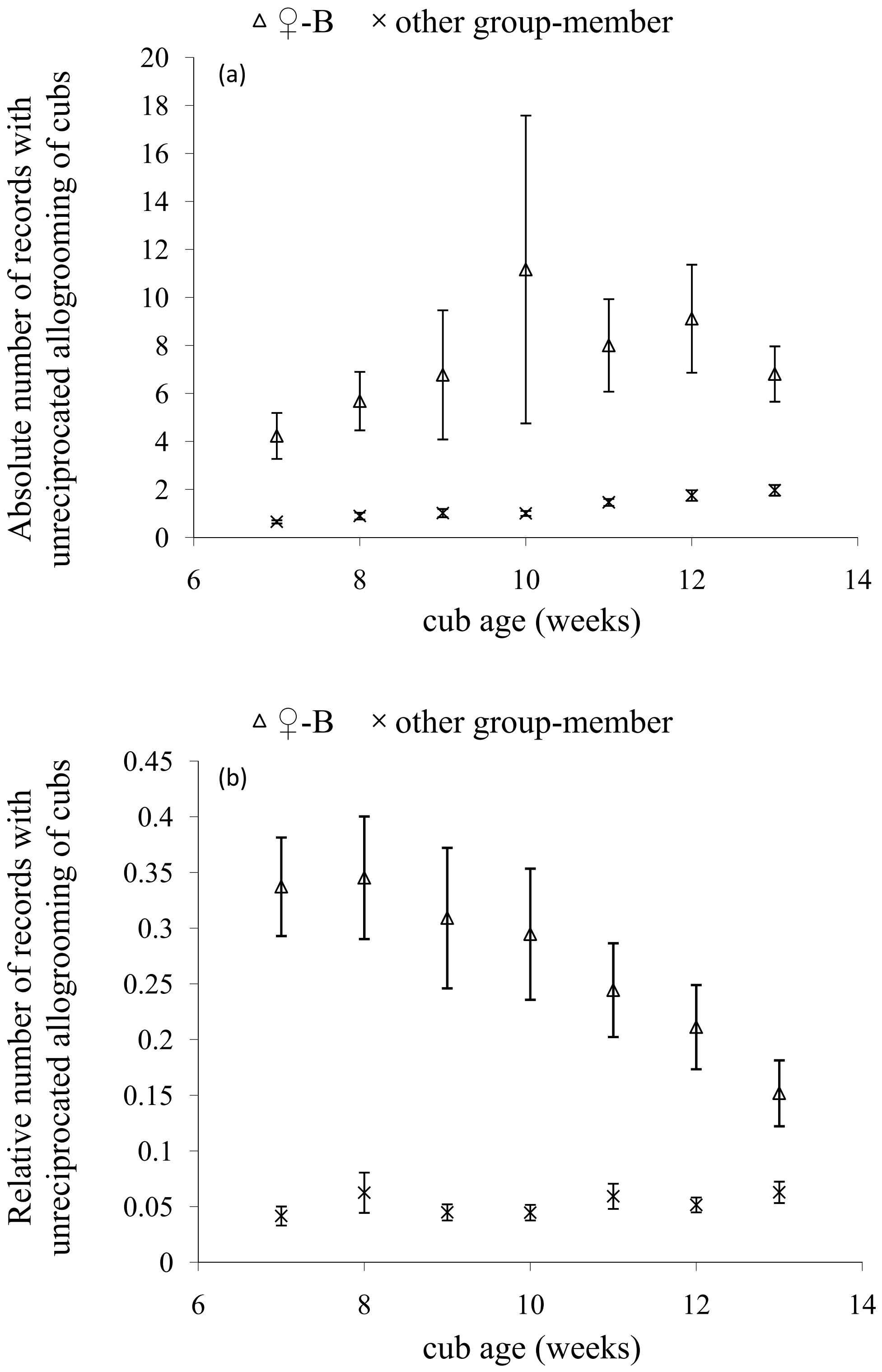
△ ♀-B × other group-member
(a)
Absolute number of records with unreciprocated allogrooming of cubs
20
18
16
14
12
10
8
6
4
2
0
6
8
10
12
14
cub age (weeks)
△ ♀-B × other group-member
(b)
Relative number of records with unreciprocated allogrooming of cubs
0.45
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
6
8
10
12
14
cub age (weeks)

Figure 3

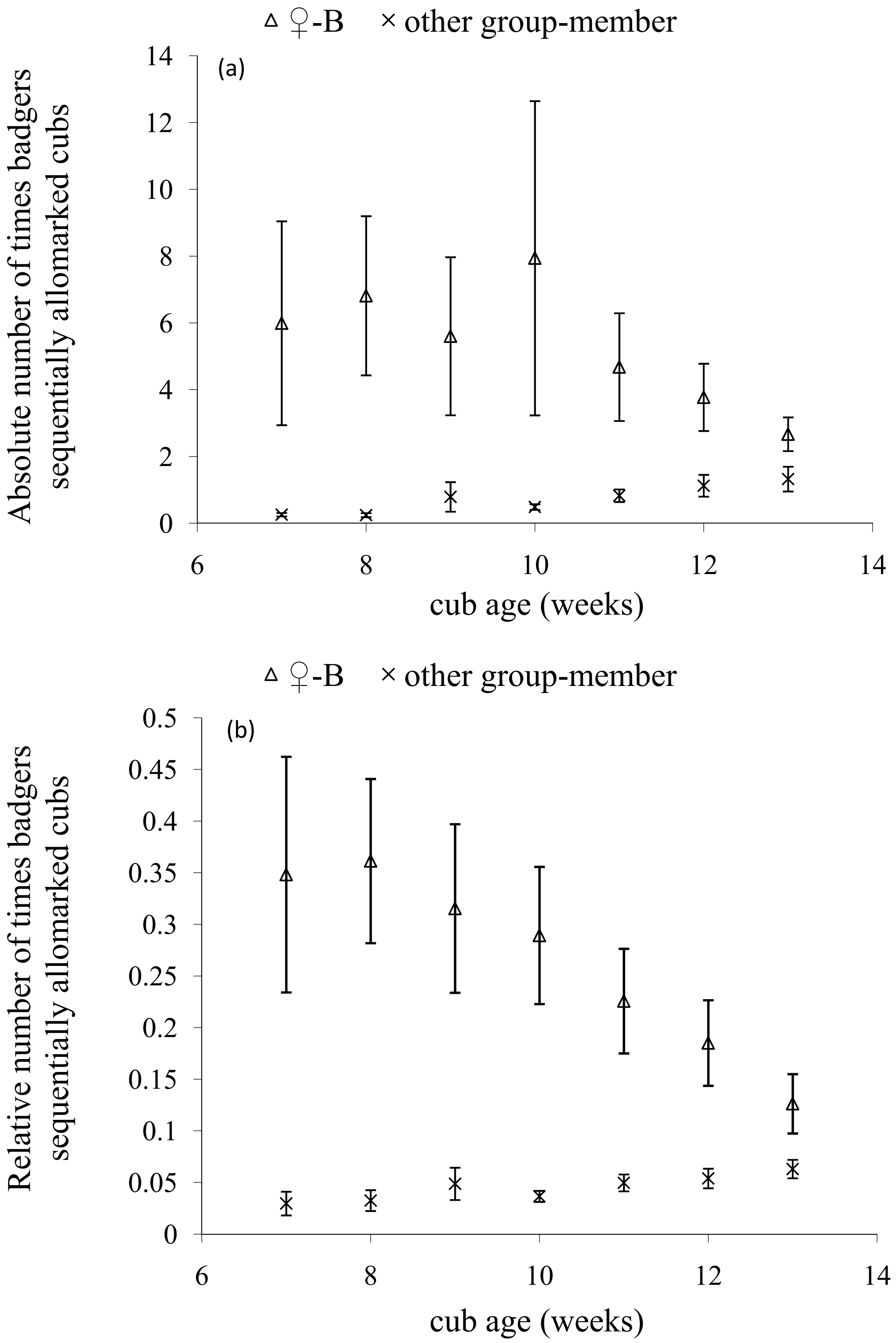
△ ♀-B × other group-member
(a)
Absolute number of times badgers sequentially allomarked cubs
0
2
4
6
8
10
12
14
6
8
10
12
14
cub age (weeks)
△ ♀-B × other group-member
(b)
Relative number of times badgers sequentially allomarked cubs
0
0.05
0.1
0.15
0.2
0.25
0.3
0.35
0.4
0.45
0.5
6
8
10
12
14
cub age (weeks)

Figure 4

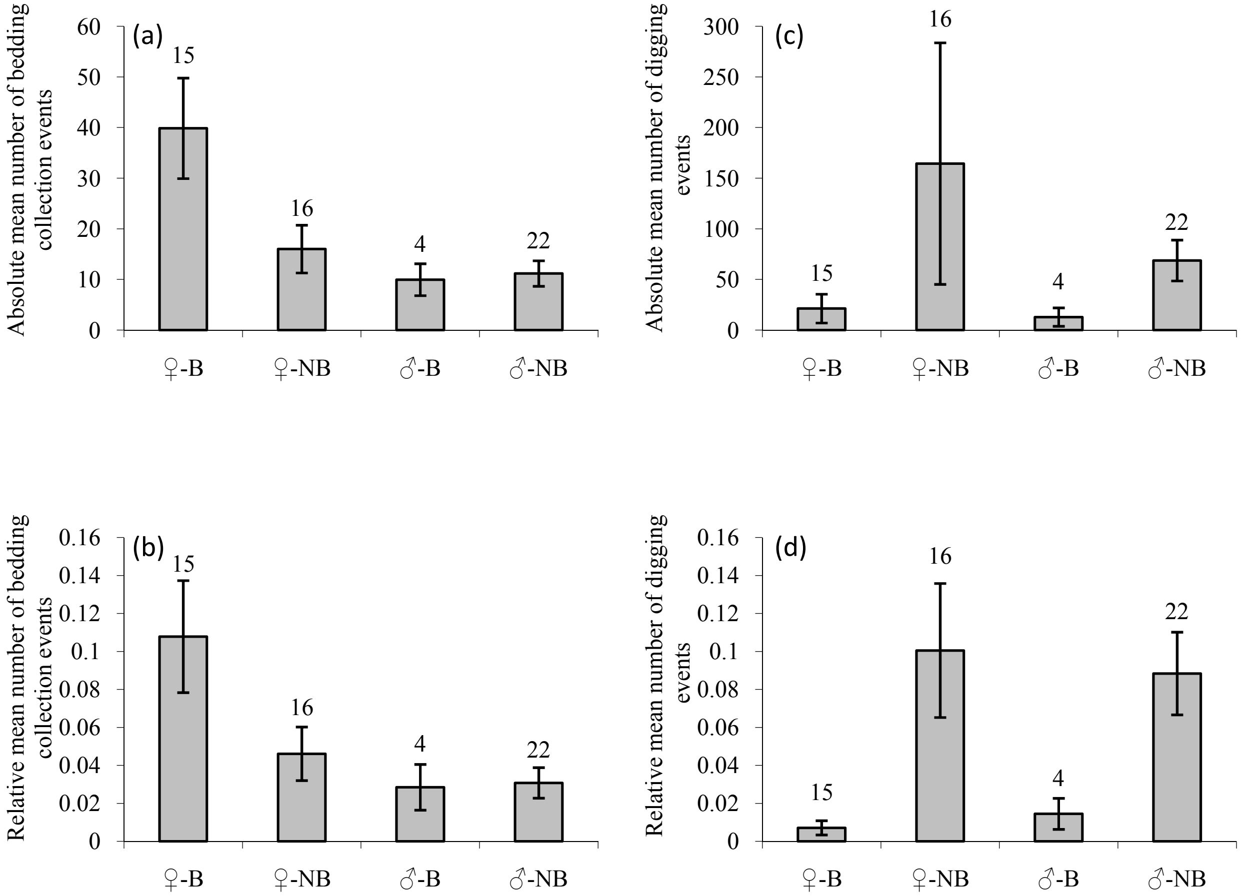
(a)
Absolute mean number of bedding collection events
0
10
20
30
40
50
60
15
16
4
22
♀-B
♀-NB
♂-B
♂-NB
(c)
Absolute mean number of digging events
0
50
100
150
200
250
300
15
16
4
22
♀-B
♀-NB
♂-B
♂-NB
(b)
Relative mean number of bedding collection events
0
0.02
0.04
0.06
0.08
0.1
0.12
0.14
0.16
15
16
4
22
♀-B
♀-NB
♂-B
♂-NB
(d)
Relative mean number of digging events
0
0.02
0.04
0.06
0.08
0.1
0.12
0.14
0.16
15
16
4
22
♀-B
♀-NB
♂-B
♂-NB

Table 1. Composition of each social-group-year, showing the maximum number of badgers in each category seen on screen at the same time as cubs. P = Pasticks; SH = Sunday's Hill; PO = Pasticks Outlier.

year		1995		2004		2005	
mean birth date		04-Feb		17-Feb		03-Feb	
social group		P	SH	P	PO	P	PO
total observation time (h)		1 383	1 242	2 444	798	3 872	1 491
cub observation time (h)		14	12	11	4	25	9
first emergence		13-Apr	26-Feb	14-Mar	23-Apr	09-Mar	25-Mar
cubs		6	3	3	1	6	5
adult females:	breeding	4	2	2	1	4	2¥
	non-breeding	4†	1^^	2**	3	1	1
adult males:	breeding[+]	2†¥	1	0	1	0	0
	non-breeding[+]	4^†¥	5	2*(+1)[$]	1*	1*	2
yearling:	females	0	1	0	0	2	1
	males	0	4	0	1	1	0
unmarked (total seen on screen)		5	4	2	1	2	3
badgers known to be unmarked		5[a]	4[b]	1[c]	1[d]	0	3[e]
group size (excl. cubs & incl. known unmarked badgers)		19	18	8	8	9	9

† One of these individuals was not clip-marked until May, but was included in the analyses as they babysat cubs in May. These numbers are therefore greater by one than those reported by Hewitt et al. (2009) and these individuals are not included in the category of 'badgers known to be unmarked'.

¥ Hewitt et al. (2009) removed one individual in their analyses (due to structural zeros) and therefore the numbers reported here are greater by one.

* One additional badger was not present for all of the cub-rearing period, either because they were found dead ($N = 2$) or presumed dead as they were only seen for a maximum of 3 days and then were not seen again ($N = 3$). These badgers were excluded from the analyses and the group size estimate.

^ One more badger that was marked was present in this category, but it was not seen on screen, so they were excluded from analyses and the group size estimate.

[$] One marked badger was only seen on one night when the cubs were also seen and was not seen at the same time as cubs, so was not included in the babysitting analyses but was included in the sett maintenance and group size.

[+] Breeding male refers to the number that sired cubs within their own social group only.

The numbers of unmarked badgers were estimated by the maximum number seen on screen at any one time. Resident badgers known to be unmarked from trapping records are: [a] 5 non-breeding adult females; [b] 3 non-breeding adult males and 1 yearling female; [c] 1 non-breeding adult female; [d] 1 non-breeding adult male; and [e] 1 within-group father, 1 non-breeding adult male, and 1 breeding female. Marked badgers from neighbouring social groups were excluded from the analyses.

Table 2. Estimates and standard errors (S.E.) of the fixed effects used to model the absolute and relative number of times an individual was observed carrying a cub. Significant effects are in bold (type 1 tests).

Fixed effect		Estimate	S.E.	*F*	*df*	*P*
Absolute model						
Intercept		0.51	0.39			
Number of records with cubs		0.91	0.45	11.03	1,5	**0.021**
Footage (mins)		0.85	0.18	62.35	1,5	< **0.001**
Group size		1.30	0.59	8.18	1,5	**0.036**
Number of cubs		-0.44	0.59	0.33	1,5	0.590
Social group	P	0.00	.	1.55	2,5	0.300
	PO	1.10	0.78			
	SH	-0.64	0.88			
Category	Breeding female	0.00	.	8.00	1,5	**0.037**
	Others	-1.08	0.38			
Relative model						
Intercept		-2.66	0.50			
Number of records with cubs		0.80	0.58	0.64	1,5	0.460
Footage (mins)		1.06	0.24	51.87	1,5	< **0.001**
Group size		1.67	0.74	0.59	1,5	0.476
Number of cubs		-1.16	0.71	0.35	1,5	0.580
Social group	P	0.00	.	2.48	2,5	0.179
	PO	1.99	1.04			
	SH	-1.06	1.05			
Category	Breeding female	0.00	.	6.00	1,5	0.058
	Others	-1.23	0.50			

The random effect estimate of individual was 0.20 ± 0.20 in the absolute model and 0.57 ± 0.34 in the relative model.

Table 3. Estimates and standard errors (S.E.) of the fixed effects used to model the absolute and relative times that group members, other than breeding females, babysat cubs on their own per week (weeks 7–13) with respect to their average relatedness to within-group young. Significant effects are in bold (type 1 tests). x = interaction.

Fixed effect		Estimate	S.E.	*F*	*df*	*P*
Absolute model						
Intercept		0.78	0.19			
Number of records with cubs		0.59	0.06	116.43	1,101	< **0.0001**
Footage (mins)		-0.03	0.13	3.69	1,101	0.058
Group size		0.13	0.15	2.38	1,101	0.126
Number of cubs		0.08	0.12	1.96	1,101	0.165
Social group	P	0.00	.	1.93	2,101	0.150
	PO	0.33	0.32			
	SH	0.05	0.35			
Week		0.13	0.12	0.02	1,101	0.876
Relatedness		0.09	0.12	0.77	1,101	0.382
Category	Non-breeding ♀	0.00	.	1.67	2,101	0.194
	Non-breeding ♂	-0.21	0.13			
	Breeding ♂	-0.12	0.25			
Category x Week	Non-breeding ♀	0.00	.	1.41	2,101	0.250
	Non-breeding ♂	-0.16	0.14			
	Breeding ♂	-0.46	0.30			
Relative model						
Intercept		-4.14	0.43			
Number of records with cubs		0.74	0.10	76.50	1,76	< **0.0001**
Footage (mins)		-0.21	0.32	16.41	1,76	< **0.001**
Group size		0.49	0.31	3.48	1,76	0.066
Number of cubs		0.30	0.24	5.29	1,76	**0.024**
Social group	P	0.00	.	2.90	2,25	0.074
	PO	1.56	0.83			
	SH	0.54	0.64			
Week		0.39	0.21	0.63	1,76	0.430
Relatedness		0.13	0.26	0.26	1,76	0.613
Category	Non-breeding ♀	0.00	.	1.70	2,76	0.190
	Non-breeding ♂	-0.49	0.34			
	Breeding ♂	-0.43	0.62			
Category x Week	Non-breeding ♀	0.00	.	3.82	2,76	**0.026**
	Non-breeding ♂	-0.33	0.23			
	Breeding ♂	-1.73	0.65			

The random effect estimate of individual nested within social-group had zero variance in absolute model, and was 0.27 ± 0.13 in the relative model.

Table 4. Number of dyads (*N*) of mothers within each filmed social-group-year more likely to represent first-order relatives than unrelated individuals.

social-group-year	*N*	number significant			total significant
		*	**	***	
SH 1995	1	0	1	0	1 (100%)
P 1995	6	0	1	1	2 (33%)
PO 2004	0	–	–	–	–
P 2004	1	0	1	0	1 (100%)
PO 2005	3^	0	0	1	1 (33%)
P 2005	6	3	2	1	6 (100%)

^ One mother in PO 2005 was unmarked

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

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Table 5. Estimates and standard errors (S.E.) of the fixed effects used to model the litter size or probability of survival of mothers (assigned with 80% confidence) within a social-group-year (significant type1 tests are in bold). Interaction = number of breeding females x number of other group-members.

Response	Dataset	Fixed effect	Estimate	S.E.	*F*	*df*	*P*
Litter size	All cubs assigned a mother	Intercept	0.29	0.07			
		Age	-0.03	0.07	0.11	1,54	0.747
		Number of breeding females	-0.06	0.07	0.73	1,54	0.397
		Number of other group-members	-0.01	0.07	0.01	1,54	0.913
		Interaction	0.00	0.07	0.00	1,54	0.997
	At least one mother assigned	Intercept	0.34	0.16			
		Age	-0.01	0.03	0.09	1,95	0.764
		Number of breeding females	-0.01	0.06	0.05	1,95	0.825
		Number of other group-members	-0.02	0.06	0.10	1,95	0.757
		Interaction	0.01	0.06	0.04	1,95	0.840
Maternal survival probability	All cubs assigned a mother	Intercept	2.91	1.44			
		Age	-0.83	0.37	4.14	1,40	**0.048**
		Number of breeding females	-0.13	0.36	0.13	1,40	0.725
		Number of other group-members	0.36	0.84	2.60	1,40	0.115
		Interaction	0.09	0.32	0.07	1,40	0.789
	At least one	Intercept	1.94	0.72			

mother assigned	Age	-0.53	0.31	2.46	1,70	0.122
	Number of breeding females	0.25	0.35	0.84	1,70	0.364
	Number of other group-members	0.67	0.35	3.48	1,70	0.066
	Interaction	-0.12	0.35	0.12	1,70	0.734

The random effect estimates of social group, year and badger identity were zero in the litter size models. In the two probability of maternal survival models, the estimates of social group were null and: year = 10.27 ± 7.39, identity = zero (all cubs assigned a mum); year = 4.88 ± 3.26 and identity = 0.06 ± 1.11 (at least one mother assigned).

Table 6. Estimates and standard errors (S.E.) of the fixed effects used to model the lifetime breeding success of cubs and the probability that cubs breed (25 social groups over 18 years). Significant effects are in bold (type1 tests). Interaction = number of breeding females x number of other group-members.

Dataset	Fixed effect		Lifetime breeding success of cubs					Probability that cubs breed				
			Estimate	S.E.	*F*	*df*	*P*	Estimate	S.E.	*F*	*df*	*P*
All cubs assigned a mum	Intercept		-0.26	0.24				-1.14	0.31			
	Cub sex	Female	0.00	.	2.08	1,135	0.151	0.00	.	6.19	1,135	**0.014**
		Male	0.43	0.26				0.83	0.30			
	Number of breeding females		-0.08	0.13	0.96	1,135	0.330	-0.16	0.16	1.58	1,135	0.211
	Number of other group-members		-0.36	0.13	7.28	1,135	**0.008**	-0.52	0.22	5.65	1,135	**0.019**
	Interaction		0.01	0.14	0.00	1,135	0.969	-0.11	0.17	0.40	1,135	0.527
At least one mother assigned	Intercept		-0.40	0.20				-1.18	0.20			
	Cub sex	Female	0.00	.	3.72	1,209	0.055	0.00	.	8.89	1,209	**0.003**
		Male	0.45	0.22				0.75	0.24			
	Number of breeding females		-0.09	0.11	0.87	1,209	0.351	-0.10	0.12	0.65	1,209	0.421
	Number of other group-members		-0.28	0.11	5.92	1,209	**0.016**	-0.35	0.14	4.97	1,209	**0.027**
	Interaction		-0.10	0.13	0.54	1,209	0.462	-0.27	0.14	3.42	1,209	0.066

The random effects for natal group and year were zero in the lifetime breeding success models; maternal identity and scale parameter were: 0.21 ± 0.26, 2.55 ± 0.54 (all cubs assigned a mother) and 0.10 ± 0.21, 3.00 ±0.57 (at least one mother assigned maternity), respectively. The random effect estimates for the models of the probability that a cub bred were zero for year; maternal identity and natal group were: 0.41 ± 0.45, 0.24 ± 0.37 (all cubs assigned a mother); 0.45 ± 0.29, and zero (at least one mother assigned maternity), respectively.

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Alloparental behaviour and long-term costs of mothers tolerating other group-members in a plurally breeding mammal

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Inter-observer reliability methods, specific details of each statistical test applied, supplementary tables 1–8, and the legends of supplementary figures 1 & 2 are contained in this electronic supplementary information.

METHODS

Inter-observer Reliability

Behavioural footage were analysed by three research assistants trained by the first author, and seven volunteers who were trained by the four experienced researchers. Seventy percent of the tapes were analysed by the four experienced researchers. Individuals were first trained to score a catalogue of digitised behavioural clips. Following this, individuals were trained to analyse behavioural footage, on a one-to-one basis with an experienced researcher, for a minimum of two days. Individuals then analysed short clips of footage on their own, and these were then re-analysed in full by an experienced researcher. This continued for two weeks or until consistent scoring was seen. A random selection of tapes were reanalysed on a weekly basis, by different combinations of volunteers and experienced researchers to ensure consistency of scoring. In total 37% of the tapes were reanalysed by a different analyst to the original one, and a further 5% were reanalysed by the original analyst to correct errors picked up by the tape checking process.

Statistical Analyses

Do group members perform direct alloparental care?

We first analysed contribution to babysitting by running a MIXED procedure with the absolute logged time each badger (*N* = 41, weeks 7–13) babysat per week as the response. We also ran a GLIMMIX procedure to analyse the relative babysitting time, with the numerator response as the time each individual babysat per week and the denominator as the total amount of babysitting observed in the social-group-year each week. The age of the cubs, in weeks (covariate), and badger category (breeding female or other group-member) were included as fixed effects, as well as an interaction between them (in addition to the five control fixed effects and one random effect detailed in the general statistical methods section of the main paper).

Secondly, we compared the number of times that each individual (*N* = 22) was observed carrying a cub. Badgers that were seen on screen at the same time as cubs but that were never seen carrying cubs were recorded as having not carried cubs (*N* = 22). Nine individuals had cub carrying data in more than one year; identity was therefore included as a random effect. For the absolute analysis we summed the number of carrying events observed by each individual (*N* = 44) as a response in a GLMM, while for the relative analysis the denominator was the total number of carrying events observed in that social-group-year. Badger category (breeding female and other group-member) was included as a fixed effect (in addition to the five control fixed effects).

We then fitted the number of ‘cub and group-member records’ in which an individual (*N* = 41) allogroomed cubs without reciprocation, or the number of times they sequentially allomarked cubs as responses in the absolute analyses (GLIMMIX procedure). We also ran a GLIMMIX procedure to analyse the relative number of allogrooming of cubs without reciprocation or sequential allomarking of cubs, with the numerator response as the number of events per individual per week and the denominator as the total number of events observed in the social-group-year each week. The fixed and random effects were identical to those in the first babysitting models described above.

Do breeding females care for more young than they are assigned parentage to?

We investigated whether breeding females (*N* = 11) babysat more cubs than their assigned litter size, by counting the duration of babysitting records and the maximum number of cubs in these, when the cubs were aged six to eleven weeks old, inclusive (i.e. from emergence to the start of the weaning period). We considered only events when one babysitter was present and we ran a Wilcoxon signed rank test on the paired differences. One social-group-year was excluded from this analysis, as there was only one mother. We entered the mean times for females present in more than one social-group-year (*N* = 3). One mother was not seen babysitting (PO 2005).

We then investigated whether breeding females were observed suckling more cubs than they were assigned maternity to. In these cases we examined the chance that the female had not been assigned maternity to offspring that were her own by: 1) counting how many foetuses the female had during ultrasound earlier in the year; and, 2) examining her LOD scores (the log-likelihood ratio of the likelihood of that female being the mother relative to the likelihood of a random female) for the other cubs in that social-group-year and whether other females in the social-group-year had higher LOD scores for the cubs. We also investigated who terminated the potential bouts of allosuckling, as termination by mothers may suggest discrimination by the mother against non-offspring.

Do individuals vary their alloparental care according to their relatedness to group young?

We first ran the babysitting analyses again, as above but excluding the category of breeding females, and classifying other group-members as: non-breeding females, breeding males, or non-breeding males. We included the average relatedness (*R*) of each group member to within-group cubs as an additional fixed covariate.

We classified whether breeding females within a social-group-year were more likely to be full-siblings, or equivalent, than unrelated individuals. We compared this to the occurrence of allosuckling.

Do individuals differ in their contribution to potential indirect alloparental behaviours?

We analysed the total number of digging and bedding collections that each of the four categories of badger were observed to do over the study period (*N* = 47). Ten individuals had data from two years, so individual identity was included as random effect. The absolute digging model was over-dispersed and a NBD error distribution was selected according to AIC.

Do alloparents gain short-term or long-term fitness benefits?

We investigated whether the number of mothers or the number of other group-members within a social group influenced litter size or probability of breeding females surviving to the next year, using maternity assignments from 1988–2005 (Dugdale et al. 2007). Group size was estimated using trapping data, assuming that badgers last caught as a cub were present for one extra year, and badgers last caught as yearlings or adults were present for two years (Dugdale et al. 2007). We assigned group membership on the basis of rules described by Dugdale et al. (2007), such that badgers trapped successively in different social groups were recorded as resident in both groups for the intervening period, with the exception that badgers caught in more than one group were divided fractionally between these groups.

We analysed mothers from social-group-years in which all cubs were assigned a mother, with both 80% confidence (*N* = 277 records from 157 mothers [87 of known age, as they were caught as a cub], in 26 social groups over 18 years) and in the smaller dataset with 95% confidence (*N* = 71 records of 64 mothers [39 of known age] from 21 social groups and 15 years). Only six females in the 95% confidence dataset had repeated measures, we therefore removed duplicate measures at random and confirmed that models based on this restricted dataset produced similar results. We also analysed mothers from social-group-years including those where not all of the cubs were assigned a mother (which may underestimate litter size but represents a larger sample) with both 80% (*N* = 396 records from 196 mothers [107 of known age] in 25 social groups over 18 years) and 95% (262 records from 153 females [82 of known age] in 24 social groups over 18 years) confidence. The 95% confidence models produced similar results to the 80% confidence models and therefore only the results based on the large 80% confidence dataset are shown.

We entered the litter size of each mother as the response, fitted to a Poisson distribution with log link, and maternal age, number of mothers and number of other group-members in the social-group-year as fixed covariates, along with the interaction between the number of mothers and other group-members. Social group, year, and badger identity were entered as random effects. When analysing the probability of maternal survival to the following year, the model was similar, except a BED was fitted with a response numerator of whether the mother survived to the next year (0 or 1) and a response denominator of one.

We also analysed whether the lifetime breeding success of a cub was related to the number of mothers or other group-members present in the cub’s natal social group when the cub was born. Lifetime breeding success was calculated for badgers that were first trapped as a cub (i.e. were of known age and reached independence) and that were considered dead by the end of 2005, using parentage assignments with 80% confidence (*N* = 422 cubs, or 283 from social-group-years in which all cubs were assigned a mother). We ran a GLMM with Poisson error distribution, with the response as the total lifetime reproductive success of each cub and we included natal social group, year, and maternal identity as random effects. The fixed covariates were the number of mothers and number of other group-members in the social-group-year; we also controlled for the sex of the cub. As 53% of the badgers, whose lifetime breeding success was known, were never assigned parentage (Dugdale *et al.* 2010), we also investigated whether the number of mothers or other group-members influenced the probability of a cub breeding. The analyses were exactly as in the previous models, except that the models had BED with a response numerator of whether each cub bred (0 or 1) and a response denominator of one.

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SUPPLEMENTARY FIGURE LEGENDS

Supplementary Figure 1. Mean (a) absolute number of minutes per week, and (b) relative proportion of time per week (incorporating unmarked/unidentifiable individuals), that a breeding female (♀–B) or other group-member was observed babysitting, against cub age in weeks. Error bars display ± one standard error. The figures display the mean predicted values from GLMMs, which controlled for repeated measures of individuals nested within a social group as a random effect and the following fixed effects: the number of times an individual was seen on screen with cubs, observation time (per week, per social-group-year), group size, the number of cubs in the group and social-group identity.

Supplementary Figure 2. Mean (a) absolute number of minutes per week, and (b) relative proportion of time per week (incorporating unmarked/unidentifiable individuals), that a breeding female (♀–B) or other group-member was observed as the only babysitter or with one other babysitter, against cub age in weeks. Error bars display ± one standard error. The figures display the mean predicted values from GLMMs, which controlled for repeated measures of individuals nested within a social group as a random effect and the following fixed effects: the number of times an individual was seen on screen with cubs, observation time (per week, per social-group-year), group size, the number of cubs in the group and social-group identity.

Supplementary table 1. Estimates and standard errors (S.E.) of the fixed effects used to model the absolute and relative time (minutes) an individual was observed babysitting per week (weeks 7–13), with the whole dataset (when there were up to nine babysitters on screen). Significant effects are in bold (type 1 tests). x = interaction.

Fixed effect		Estimate	S.E.	*F*	*df*	*P*
Absolute model						
Intercept		2.50	0.15			
Number of records with cubs		0.74	0.07	183.67	1,83.3	< **0.0001**
Footage (mins)		0.16	0.12	1.78	1,44.3	0.189
Group size		0.08	0.15	0.22	1,33.7	0.644
Number of cubs		-0.03	0.12	0.06	1,69.7	0.815
Social group	P	0.00	.	1.00	2,63.7	0.372
	PO	0.17	0.28			
	SH	0.11	0.25			
Week		0.06	0.08	10.02	1,182	**0.002**
Category	Breeding female	0.00	.	8.74	1,35.2	**0.006**
	Others	-0.46	0.16			
Category x Week	Breeding female	0.00	.	9.05	1,169	**0.003**
	Others	0.34	0.11			
Relative model						
Intercept		-1.47	0.16			
Number of records with cubs		0.29	0.02	164.02	1,144	< **0.0001**
Footage (mins)		-0.02	0.06	0.08	1,144	0.782
Group size		0.04	0.13	12.76	1,144	< **0.001**
Number of cubs		-0.35	0.05	0.10	1,144	0.753
Social group	P	0.00	.	4.49	2,38	**0.018**
	PO	0.26	0.32			
	SH	-0.61	0.25			
Week		-0.56	0.03	104.67	1,144	< **0.0001**
Category	Breeding female	0.00	.	97.74	1,144	< **0.0001**
	Others	-1.37	0.14			
Category x Week	Breeding female	0.00	.	201.95	1,144	< **0.0001**
	Others	0.75	0.05			

The random effect estimate of individual nested within social-group was 0.07 ± 0.05 in the absolute analysis; in the relative analysis the estimate was 0.32 ± 0.08.

Supplementary table 2. Estimates and standard errors (S.E.) of the fixed effects used to model the absolute and relative time (m) an individual was observed babysitting per week (weeks 7–13). Significant effects are in bold (type 1 tests). x = interaction.

Fixed effect		Estimate	S.E.	*F*	*df*	*P*
Absolute model						
Intercept		1.70	0.13			
Number of records with cubs		0.85	0.07	282.26	1,182	< **0.0001**
Footage (mins)		0.16	0.14	0.20	1,182	0.654
Group size		0.25	0.15	0.17	1,182	0.680
Number of cubs		-0.17	0.12	0.15	1,182	0.702
Social group	P	0.00	.	3.35	2,182	**0.037**
	PO	0.57	0.26			
	SH	0.01	0.25			
Week		-0.14	0.09	3.77	1,182	0.054
Category	Breeding female	0.00	.	39.18	1,182	< **0.0001**
	Others	-0.86	0.14			
Category x Week	Breeding female	0.00	.	3.63	1,182	0.058
	Others	0.23	0.12			
Relative model						
Intercept		-1.43	0.28			
Number of records with cubs		0.27	0.03	83.01	1,144	< **0.0001**
Footage (mins)		0.14	0.09	2.09	1,144	0.151
Group size		0.46	0.23	0.34	1,144	0.561
Number of cubs		-0.61	0.08	1.33	1,144	0.251
Social group	P	0.00	.	3.99	2,38	**0.027**
	PO	0.78	0.56			
	SH	-0.35	0.43			
Week		-0.39	0.04	13.43	1,144	**0.001**
Category	Breeding female	0.00	.	99.63	1,144	< **0.0001**
	Others	-2.62	0.27			
Category x Week	Breeding female	0.00	.	73.42	1,144	< **0.0001**
	Others	0.90	0.10			

The random effect estimate of individual nested within social group had zero variance in the absolute model and was 0.85 ± 0.25 in the relative model.

Supplementary table 3. Estimates and standard errors (S.E.) of the fixed effects used to model the absolute and relative time (minutes) an individual was observed babysitting per week (weeks 7–13), when there were up to two babysitters on screen. Significant effects are in bold (type 1 tests). x = interaction.

Fixed effect		Estimate	S.E.	*F*	*df*	*P*
Absolute model						
Intercept		2.17	0.13			
Number of records with cubs		0.80	0.07	246.6	1,182	< **0.0001**
Footage (mins)		0.09	0.14	0.06	1,182	0.811
Group size		0.10	0.15	1.17	1,182	0.280
Number of cubs		-0.09	0.13	0.30	1,182	0.586
Social group	P	0.00	.	2.40	2,182	0.094
	PO	0.48	0.26			
	SH	-0.02	0.26			
Week		-0.05	0.09	1.82	1,182	0.179
Category	Breeding female	0.00	.	30.65	1,182	< **0.0001**
	Others	-0.78	0.14			
Category x Week	Breeding female	0.00	.	0.87	1,182	0.353
	Others	0.11	0.12			
Relative model						
Intercept		-1.34	0.19			
Number of records with cubs		0.26	0.02	130.98	1,144	< **0.0001**
Footage (mins)		-0.01	0.07	1.45	1,144	0.230
Group size		0.17	0.16	6.50	1,144	**0.012**
Number of cubs		-0.46	0.06	0.74	1,144	0.391
Social group	P	0.00	.	4.71	2,38	**0.015**
	PO	0.50	0.38			
	SH	-0.49	0.30			
Week		-0.44	0.03	52.27	1,144	< **0.0001**
Category	Breeding female	0.00	.	128.32	1,144	< **0.0001**
	Others	-1.93	0.17			
Category x Week	Breeding female	0.00	.	99.53	1,144	< **0.0001**
	Others	0.70	0.07			

The random effect of individual nested within social-group was removed in the absolute analysis as its variance estimate was zero; in the relative analysis the estimate was 0.42 ± 0.12.

Supplementary table 4. Estimates and standard errors (S.E.) of the fixed effects used to model the absolute and relative number of ‘cub and group-member records’ an individual was observed allogrooming cubs without reciprocation per week (weeks 7–13). Significant effects are in bold (type 1 tests). x = interaction.

Fixed effect		Estimate	S.E.	*F*	*df*	*P*
Absolute model						
Intercept		1.33	0.14			
Number of records with cubs		0.33	0.02	302.63	1,144	< **0.0001**
Footage (mins)		-0.03	0.09	11.92	1,144	< **0.001**
Group size		-0.48	0.13	10.11	1,144	**0.002**
Number of cubs		0.04	0.09	0.41	1,144	0.523
Social group	P	0.00	.	0.28	2,38	0.761
	PO	-0.33	0.28			
	SH	0.47	0.25			
Week		0.11	0.05	1.49	1,144	0.224
Category	Breeding female	0.00	.	50.07	1,144	< **0.0001**
	Others	-1.14	0.16			
Category x Week	Breeding female	0.00	.	2.51	1,144	0.115
	Others	0.17	0.11			
Relative model						
Intercept		-1.62	0.19			
Number of records with cubs		0.25	0.03	99.73	1,144	< **0.0001**
Footage (mins)		-0.10	0.12	1.14	1,144	0.286
Group size		-0.08	0.17	7.14	1,144	**0.008**
Number of cubs		-0.23	0.11	0.58	1,144	0.449
Social group	P	0.00	.	1.33	2,38	0.277
	PO	0.50	0.39			
	SH	0.10	0.32			
Week		-0.44	0.06	29.02	1,144	< **0.0001**
Category	Breeding female	0.00	.	63.79	1,144	< **0.0001**
	Others	-1.64	0.21			
Category x Week	Breeding female	0.00	.	18.33	1,144	< **0.0001**
	Others	0.52	0.12			

The random effect estimate of individual nested within social group was 0.10 ± 0.07 in the absolute model and 0.26 ± 0.11 in the relative model.

Supplementary table 5. Estimates and standard errors (S.E.) of the fixed effects used to model the absolute and relative number of times an individual was observed sequentially allomarking cubs per week (weeks 7–13). Significant effects are in bold (type 1 tests). x = interaction.

Fixed effect		Estimate	S.E.	*F*	*df*	*P*
Absolute model						
Intercept		0.86	0.23			
Number of records with cubs		0.33	0.03	105.38	1,144	< **0.0001**
Footage (mins)		0.23	0.12	26.23	1,144	< **0.0001**
Group size		-0.13	0.19	0.16	1,144	0.687
Number of cubs		0.01	0.13	0.05	1,144	0.818
Social group	P	0.00	.	2.21	2,38	0.123
	PO	-1.08	0.51			
	SH	-0.24	0.39			
Week		-0.22	0.06	0.05	1,144	0.821
Category	Breeding female	0.00	.	15.43	1,144	< **0.001**
	Others	-1.04	0.27			
Category x Week	Breeding female	0.00	.	18.20	1,144	< **0.0001**
	Others	0.60	0.14			
Relative model						
Intercept		-1.75	0.29			
Number of records with cubs		0.29	0.05	43.49	1,144	< **0.0001**
Footage (mins)		-0.07	0.17	0.02	1,144	0.890
Group size		-0.07	0.24	1.99	1,144	0.161
Number of cubs		-0.26	0.17	0.30	1,144	0.587
Social group	P	0.00	.	0.23	2,38	0.795
	PO	0.05	0.66			
	SH	-0.19	0.47			
Week		-0.54	0.07	11.29	1,144	**0.001**
Category	Breeding female	0.00	.	21.23	1,144	< **0.0001**
	Others	-1.43	0.32			
Category x Week	Breeding female	0.00	.	23.65	1,144	< **0.0001**
	Others	0.77	0.16			

The random effect estimate of individual nested within social group was 0.39 ± 0.17 in the absolute model and 0.65 ± 0.24 in the relative model.

Supplementary table 6. Estimates and standard errors (S.E.) of the fixed effects used to model the absolute and relative times that group members, other than breeding females, babysat cubs per week (weeks 7–13), when there were up to two babysitters on screen, with respect to their average relatedness to within-group young. Significant effects are in bold (type 1 tests). x = interaction.

Fixed effect		Estimate	S.E.	*F*	*df*	*P*
Absolute model						
Intercept		1.15	0.21			
Number of records with cubs		0.73	0.07	121.26	1,101	< **0.0001**
Footage (mins)		-0.12	0.14	0.84	1,101	0.363
Group size		-0.07	0.17	1.90	1,101	0.171
Number of cubs		0.04	0.13	0.73	1,101	0.396
Social group	P	0.00	.	0.01	2,101	0.992
	PO	0.22	0.36			
	SH	0.12	0.39			
Week		0.06	0.14	2.03	1,101	0.157
Relatedness		-0.10	0.14	0.47	1,101	0.493
Category	Non-breeding ♀	0.00	.	0.09	101	0.910
	Non-breeding ♂	-0.04	0.15			
	Breeding ♂	0.06	0.28			
Category x Week	Non-breeding ♀	0.00	.	1.11	101	0.332
	Non-breeding ♂	-0.19	0.15			
	Breeding ♂	-0.40	0.33			
Relative model						
Intercept		-3.67	0.30			
Number of records with cubs		0.62	0.07	72.31	1,76	< **0.0001**
Footage (mins)		-0.50	0.15	23.13	1,76	< **0.0001**
Group size		-0.09	0.19	4.02	1,76	**0.048**
Number of cubs		0.05	0.14	2.53	1,76	0.116
Social group	P	0.00	.	0.01	2,25	0.993
	PO	0.72	0.46			
	SH	0.42	0.46			
Week		0.15	0.13	2.23	1,76	0.140
Relatedness		-0.33	0.19	2.40	1,76	0.126
Category	Non-breeding ♀	0.00	.	0.01	2,76	0.991
	Non-breeding ♂	0.03	0.24			
	Breeding ♂	0.32	0.44			
Category x Week	Non-breeding ♀	0.00	.	6.01	2,76	**0.004**
	Non-breeding ♂	-0.24	0.14			
	Breeding ♂	-1.46	0.44			

The random effect estimate of individual nested within social-group had zero variance in absolute model, and was 0.16 ± 0.08 in the relative model.

Supplementary table 7. Estimates and standard errors (S.E.) of the fixed effects used to model the absolute and relative number of times an individual was observed carrying bedding. Significant effects are in bold (type1 tests).

Fixed effect		Estimate	S.E.	*F*	*df*	*P*
Absolute model						
Intercept		1.81	0.35			
Number of times observed		0.52	0.14	10.80	1,6	**0.017**
Group size		-0.12	0.31	2.51	1,6	0.164
Number of cubs		-0.07	0.05	1.57	1,6	0.257
Social group	P	0.00	.	0.79	2,6	0.498
	PO	0.75	0.64			
	SH	0.35	0.55			
Category	Breeding ♀	0.00	.	0.90	3,6	0.494
	Non-breeding ♀	0.23	0.20			
	Breeding ♂	0.05	0.77			
	Non-breeding ♂	-0.38	0.45			
Relative model						
Intercept		-4.03	0.36			
Number of times observed		0.60	0.15	13.55	1,6	**0.010**
Group size		-0.06	0.32	6.21	1,6	**0.047**
Number of cubs		-0.26	0.06	2.86	1,6	0.142
Social group	P	0.00	.	1.26	2,6	0.349
	PO	0.95	0.65			
	SH	-0.16	0.57			
Category	Breeding ♀	0.00	.	0.98	3,6	0.460
	Non-breeding ♀	0.26	0.21			
	Breeding ♂	0.03	0.79			
	Non-breeding ♂	-0.40	0.46			

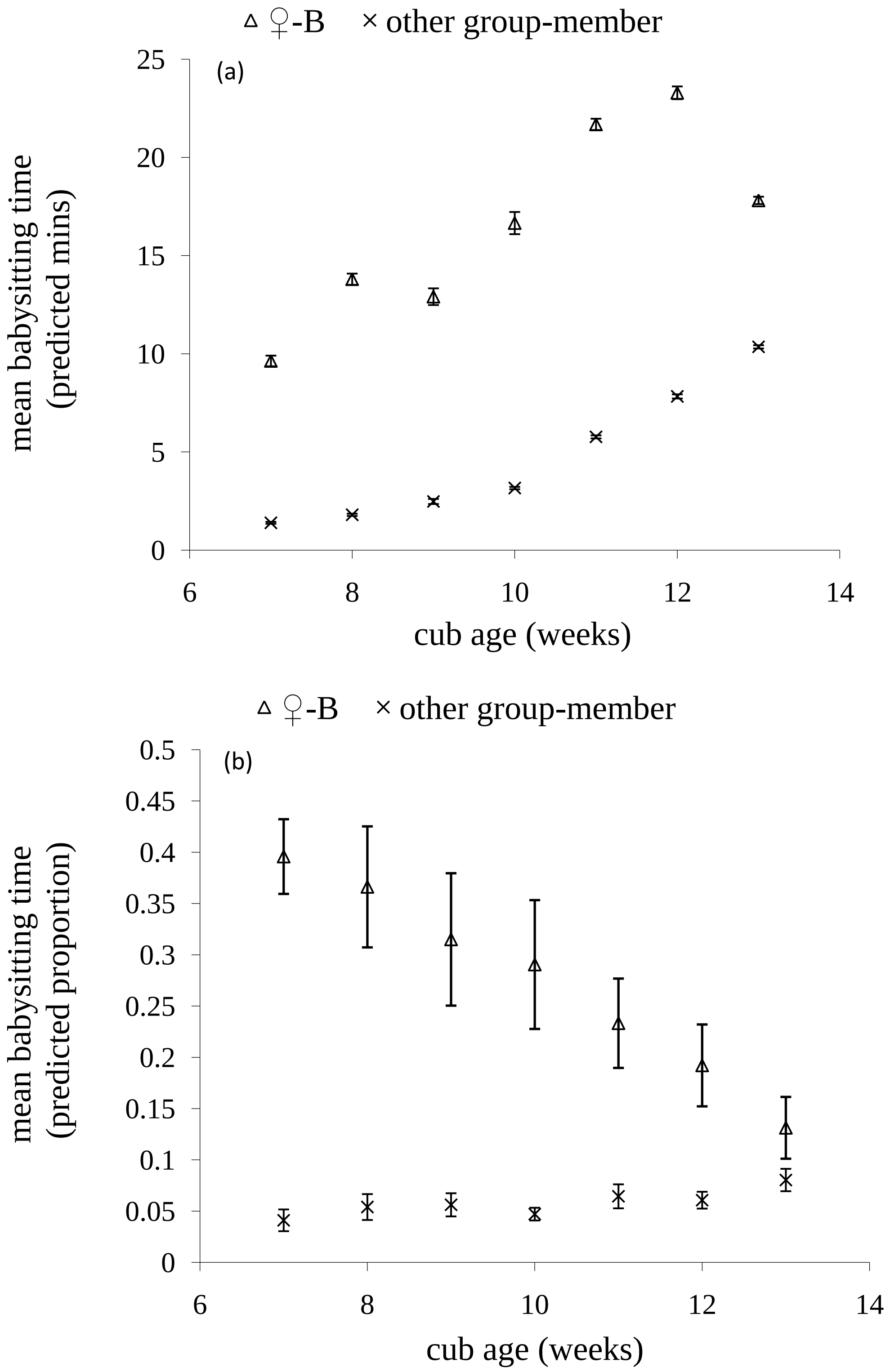
The random effect estimate of individual was 1.63 ± 0.50 in the absolute model and 1.71 ± 0.53 in the relative model.

Supplementary table 8. Estimates and standard errors (S.E.) of the fixed effects used to model the absolute and relative number of times an individual was observed digging. Significant effects are in bold (type1 tests).

Fixed effect		Estimate	S.E.	*F*	*df*	*P*
Absolute model						
Intercept		-0.37	0.57			
Number of times observed		1.80	0.53	7.26	1,6	**0.036**
Group size		0.47	0.45	5.16	1,6	**0.064**
Number of cubs		-0.59	0.34	3.26	1,6	0.121
Social group	P	0.00	.	1.45	2,6	0.305
	PO	0.39	0.63			
	SH	-2.03	0.88			
Category	Breeding ♀	0.00	.	19.23	3,6	**0.002**
	Non-breeding ♀	4.32	0.67			
	Breeding ♂	3.43	1.03			
	Non-breeding ♂	4.59	0.65			
Relative model						
Intercept		-7.40	0.73			
Number of times observed		0.37	0.10	6.70	1,6	**0.041**
Group size		-1.64	0.63	14.45	1,6	**0.009**
Number of cubs		0.07	0.08	0.39	1,6	0.554
Social group	P	0.00	.	0.20	2,6	0.821
	PO	-0.10	1.13			
	SH	-0.47	1.08			
Category	Breeding ♀	0.00	.	12.70	3,6	**0.005**
	Non-breeding ♀	2.52	0.48			
	Breeding ♂	2.36	1.52			
	Non-breeding ♂	4.29	0.92			

The random effect estimate of individual was zero in the absolute model (scale = 2.01 ± 0.43) and 5.40 ± 1.89 in the relative model.

Supplementary Figure 1



Supplementary Figure 2