Grandmotherly care: a case study in Indian free-ranging dogs

Manabi Paul, Sreejani Sen Majumder & Anindita Bhadra

Springer

ARTICLE
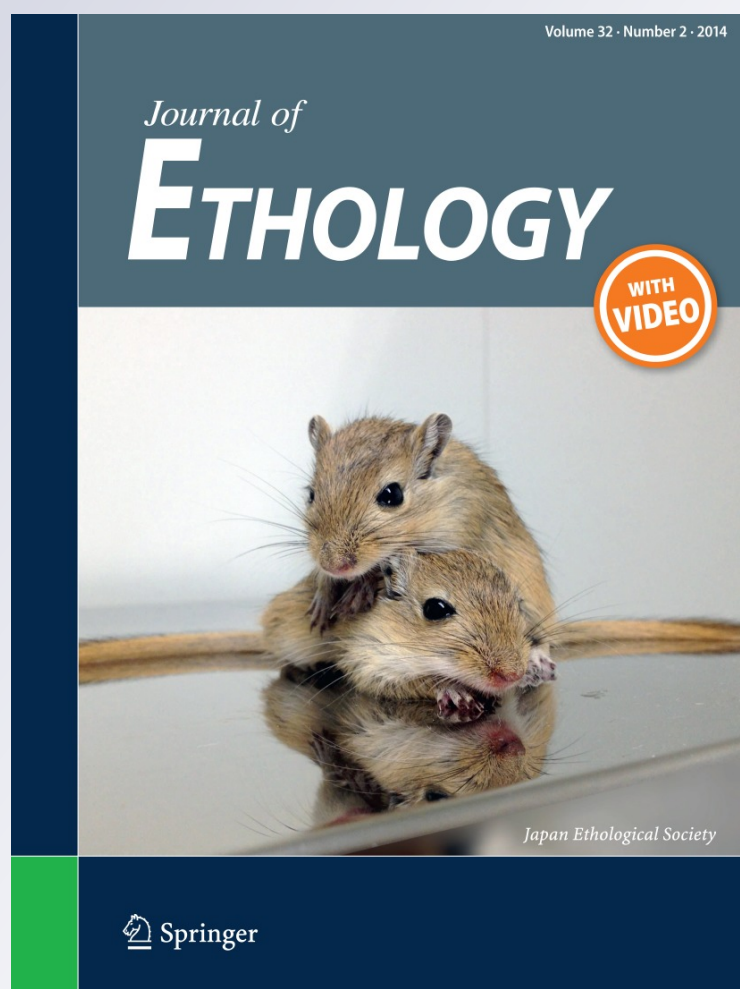
Grandmotherly care: a case study in Indian free-ranging dogs

**Manabi Paul · Sreejani Sen Majumder ·
Anindita Bhadra**

Abstract Parental care is an essential component in the life history of mammals. In group-living species, care can be provided by adults other than the parents, and such care is termed alloparental care. Alloparental care is known in a wide spectrum of species, from insects to humans. Most canids that live in stable packs demonstrate cooperative breeding, where subordinates provide care to the offspring of the dominants, without reproducing themselves. Free-ranging dogs in India have a dynamic social system and, unlike their cooperatively breeding ancestors, the grey wolves, all adults in a dog group have equal mating opportunities. This at times leads to the birth of multiple litters within an existing dog group. In this paper, we report the first field observations of alloparental care made on a dog group where a bitch provided care to her grandpups, through interactions other than suckling. The allomaternal care acted as a supplement to the care provided by the mother, and was thus beneficial to the pups.

Keywords Alloparental care · Social · Dogs · Pups · Cooperative breeding

M. Paul · S. S. Majumder · A. Bhadra (✉)
Behaviour and Ecology Lab, Department of Biological Sciences,
Indian Institute of Science Education and Research,
P.O. BCKV Main Campus, Mohanpur, Nadia, 741252 Kolkata,
West Bengal, India
e-mail: abhadra@iiserkol.ac.in

Introduction

Parental care plays an important role in the development of the young in mammals. Even in species where mothers do not provide care in the form of dens and protection, mothers suckle their offspring, from birth to weaning. Parental care in mammals begins from gestation, and often continues beyond the weaning stage, especially in social species (Gubernick 1981; Clutton-Brock 1991). Though care is most often provided by the mother alone (Kleiman and Malcolm 1981), paternal care is also known to exist in some species including humans (Kleiman and Malcolm 1981; Woodroffe and Vincent 1994), and care by other adults, especially in group-living species, is also known (Riedman 1982; Jennions and Macdonald 1994). Social canids like wolves (*Canis lupus lupus*), coyotes (*Canis latrans*), Arctic foxes (*Vulpes lagopus*), African wild dogs (*Lycaon pictus*), etc. live in packs which hunt together, and cooperative breeding is a common feature in such packs (Estes and Goddard 1967; Mech 1970; Ewer 1973; Fox et al. 1975; Jennions and Macdonald 1994; Clutton-Brock 2006). However, in non-pack dwelling canids, such cooperative breeding is unknown (Sandell 1989; Kleiman 2011).

Domestic dogs (*Canis lupus familiaris*) are generally thought to have evolved from grey wolves thousands of years ago (Scott and Fuller 1965; Beck 1975; Clutton-Brock 1995). Dogs display a wide range of social organization, from solitary living in human homes to living in small mixed groups as farm animals, to living in packs as free-ranging and feral dogs (Macdonald 1979; Berman and Dunbar 1983; Serpell 1995; Sillero-Zubiri et al. 2004). Parental care has been reported in both domestic dogs (Scott and Marston 1950; Welker 1959; Rheingold 1963; Kleiman and Malcolm 1981) and free-ranging dogs (Pal

2005), but there are no reports of cooperative breeding in dog groups. Free-ranging dogs are known to live in stable social groups in which all adults have mating opportunities (Pal 2011), and grouping patterns are often influenced by mating interests (Sen Majumder et al. 2013). Pups stay with the natal group until sexual maturity, and dispersals are common, though not compulsory, in the sub-adult and adult phases of life (Pal et al. 1998). Hence, the free-ranging dogs are a good model system for understanding social dynamics in canids, but have so far rarely been studied.

We have embarked on a long-term study of the eco-ethology of free-ranging dogs in India where natural populations of dogs exist on the streets, co-habiting with humans (Vanak et al. 2009). These dogs are scavengers, living off human excesses in all habitations, from cities to forest fringes (Vanak and Gompper 2009; Vanak et al. 2009). Though the dogs defend territories as groups, most often they tend to forage alone, which no doubt is a good strategy for a scavenging lifestyle. However, when juveniles are present in the population, larger foraging units are seen, and, in the mating season, male–female pairs often forage together. Hence, there is a lot of plasticity in the social behaviour of the dogs, and social interests may override the tendency to at times compete over food (Sen Majumder et al. 2013). Though the dogs are chiefly scavengers, reports of free-ranging dogs hunting as a pack are sometimes encountered (Kaushik 2008; Achappa 2012; Oppili 2013). We have records of five such kills by dogs on the transit campus of IISER-K, which is a semi-urban habitat, with goats, cows and pigs grazing in open fields. The dogs attacked and killed rats and juvenile goats and pigs in a coordinated fashion, highly reminiscent of cooperative hunting, where two or three dogs surrounded the prey from different directions, barking loudly, and chased it, closing in the circle to finally kill it (Kruuk 1975; Peterson and Ciucci 2003). Hence the dogs seem to have retained the ability for cooperative hunting from their ancestral condition (Macdonald 1979, 1983; Sillero-Zubiri et al. 2004), though they do not usually hunt, perhaps because such attempts are typically thwarted by people. Even when they do kill, they are rarely seen to eat their kill as they are immediately chased off by people (personal observations). Though cooperative hunting is reported in dogs, cooperative breeding has never been reported in these canids.

We are presently carrying out a long-term field-based population-level study on parental care in the free-ranging dogs. During the course of this study, we observed an interesting family group over two denning seasons. Here, we report our first field observation of alloparental care in this family group that began with a pregnant female who established a territory in an area then unoccupied by dogs.

Materials and methods

Study site

This work was carried out in the IISER-Kolkata transit campus at Mohanpur (22°94′N, 88°53′E), West Bengal, India, which has an interesting mixture of urban and rural characters. We carried out this study in the area around the J.C. Bose building (JCB), which is close to a number of food stalls. Buildings on campus are interspersed with agricultural fields, and thus resources for dogs are patchy, being concentrated around offices, research laboratories and houses. This study was conducted in an area of 5.98 ha containing two major food sources—the Annex canteen and Dhaba1. There were two resources immediately outside the study area—the Club quarters on one side, and the Masi's Dhaba on the other. The shaded grey zone shows the territory of the focal group, while the entire map shows the maximum home range in both seasons (Fig. 1). The area (5.98 ha) was occupied by 5 adults (2 M, 3 F) and 7 pups (2 M, 5 F) in season 1, and by 13 adults (4 M, 9 F) and 15 pups (6 M, 9 F) in season 2, including the subjects of this study. ML used a space under a flight of stairs on the terrace of the MTS building as her den in season 1, while PW used a similar site on the terrace of the LEL building as her den in season 2. MTS and LEL are buildings with similar plans separated by a small lane (ESM Fig. 1). Geographical coordinates were measured using a Garmin eTrex 30 GPS device. The positional data was compiled using 'Garmin Basecamp' and the territory was delineated
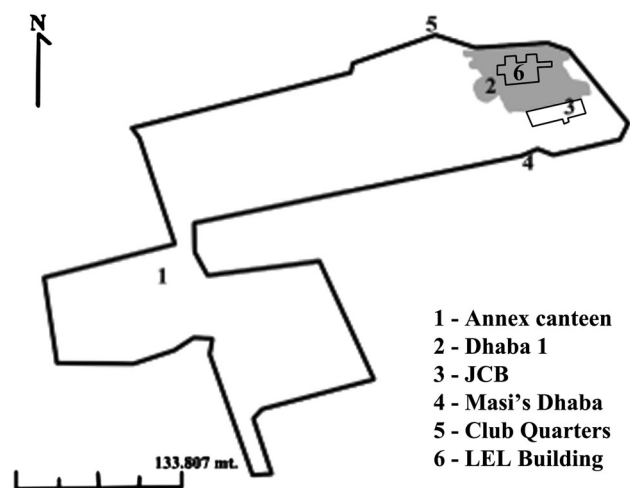
Fig. 1 The territory and home range of the focal dog group on the transit campus of IISER-K at Mohanpur (22°94′N, 88°53′E), West Bengal, India. The *black line* demarcates the home range (the study site), and the *grey area* denotes the territory of the focal group. Relevant landmarks are also shown. The map is drawn to scale using the original image produced using the GPS readings and the Google Earth map, provided as supplementary material (ESM Fig. 2)

1 - Annex canteen
2 - Dhaba 1
3 - JCB
4 - Masi's Dhaba
5 - Club Quarters
6 - LEL Building

133.807 mt.

on Google Earth. The detailed map thus created has been provided as supplementary material (ESM Fig. 2).

Focal individual

An adult female free-ranging dog (ML) was observed between December 2010 and April 2012. Until October 2010, there were only three adult dogs (one male and two females) in the area around JCB, among which only one female stayed near Dhaba 1. ML was pregnant when she came to the study site at the end of October 2010 and occupied the area in front of Dhaba 1, claiming it as her territory (Fig. 1). The three resident dogs never entered the area that ML claimed as her territory (grey shaded area in Fig. 1), but they had overlapping home ranges. ML did not form a social bond with any of the existing dogs, and defended her territory alone. ML mated with two males, BL and BR, from adjacent territories in both mating seasons. All the dogs mentioned here were present within the study area of 5.98 ha.

Observations

We carried out behavioural observations in two consecutive denning seasons. In the first season, the focal group consisted of ML and her offspring—PB (male) and PW (female). ML had mated in the second season, but was pseudopregnant (Allen 1986; Gobello et al. 2001a, b). PW had been observed to mate with BL, and had probably also mated with BR (mating attempts observed, but locking not observed) in 2012 (ESM Fig. 2). In the second season, the focal group consisted of ML, PW and PW's pups, BR and WH (both males). In the first season, we carried out observations on the focal group from the 8th to 12th weeks of pup age (19 January to 17 February 2011), as at this time we were interested in studying the interactions between the mother and pups during weaning, which occurs around 10–11 weeks (Pal 2008). We observed the focal group for three consecutive days in a week, in two sessions, morning (0930–1130 hours) and evening (1300–1500 hours), using an equal number of instantaneous scans and all occurrences sessions (AOS). In the second season, we carried out observations from the 3rd to 13th weeks of pup age (5 February to 19 April 2012). There were two morning and two evening sessions spread over every 2 weeks, and each session was of 3 h (0900–1200 hours; 1400–1700 hours), consisting of equal numbers of scans and AOS. Thus, we obtained 60 h data consisting of 360 scans and AOS each in the first season and 66 h data consisting of 396 scans and AOS each in the second season.

Interactions of the members of the focal group with any other dogs, animals like cows, goats, etc. and even humans were recorded. We pooled all instances of suckling,

Table 1 Behaviours used to score for parental and alloparental care, sorted according to the various categories used in the analysis. The sum of all the listed behaviours was used to calculate the time spent with the pups. In cases of alloparental care, we observed at least one instance of all the above behaviours other than suckling

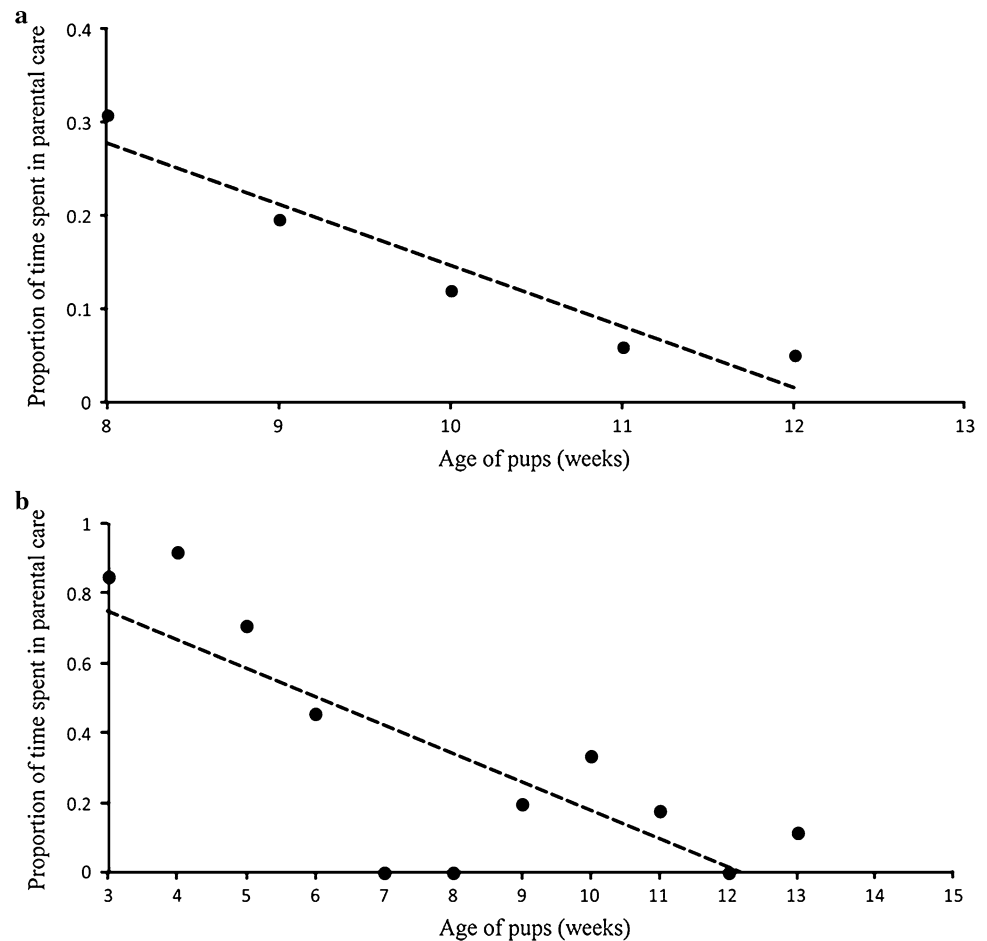| Active parental care		Passive parental care
Guarding	Others	
Threaten	Suckling	Sitting and watching object/ individual
Barking	Allogrooming	Standing and watching object/ individual
Angry barking	Providing regurgitated food	Walking and watching object/ individual
Fighting	Offering food	Pile sleeping
Chasing	Playing	Sleeping/lazing
Alert		Smelling ground

allogrooming, playing, pile-sleeping, providing regurgitated food and guarding pups into the category of active parental care. We calculated the proportion of time spent by the mother in active parental care from the scan data, and the rate (frequency per hour) at which each of the behaviours was shown from the AOS data. We also calculated the proportion of time spent with the pups in behaviours other than those listed above as a measure of passive protection provided by the mother simply by her presence with the pups as passive parental care. The same behaviours shown towards the pups by the grandmother were scored as alloparental care. A list of all the behaviours used in the analysis under different subheads has been provided in Table 1. All statistical analysis was carried out using statistiXL v.1.8.

Results

Parental care

We obtained data on parental care for ML in the first season and for PW, her daughter, in the second season. In the first week of observations, ML spent 18.05 % of her time with her pups, of which 5.55 % was devoted to active parental care. The time spent in active parental care decreased significantly as the pups grew from 8 to 12 weeks (linear regression: $R^2 = 0.922$, $\beta = -0.960$, $p = 0.009$) (Fig. 2a), though the total proportion of time that the mother spent with them did not (linear regression: $R^2 = 0.202$, $\beta = 0.449$, $p = 0.448$). PW and her pups were observed for a longer period, and, in the first week of observations, when the pups were in their 3rd week, she spent 65 % of her time with them, of which 84.6 % was

Fig. 2 The proportion of time spent in parental care by the mothers **a** ML and **b** PW, at different ages (in weeks) of the pups. The *regression lines* are shown in the figure

spent in active parental care. Considering the entire period of observations from the 3rd to the 13th weeks of pup age, the time spent with pups did not vary significantly ($R^2 = 0.039$, $\beta = 0.197$, $p = 0.561$), though the proportion of time spent in active parental care out of the time spent with pups reduced significantly with pup age (linear regression: $R^2 = 0.618$, $\beta = -0.786$, $p = 0.004$) (Fig. 2b). The time spent in active parental care by ML and PW in the weaning period, from the 8th to 12th weeks of pup age, was comparable (Mann–Whitney U test: $U = 13.0$, $df = 5, 5$, $p = 1.00$).

In the first couple of weeks of life, pups do not have the faculty of vision or hearing, and they are completely dependent on their mothers for survival. At this stage, the mother spends most of her time with the pups, only venturing out for short foraging trips (Pal 2008). We did not conduct observations at this stage as the mother and pups are mostly huddled together inside the den, and are difficult to observe. The most energy-consuming and important behaviour included under the category of parental care is suckling. Mothers typically lose weight when they suckle, due to the high energy demands of milk production (Rogowitz 1996; Dewey 1997; Dewey 1998). As the pups

grew, suckling decreased significantly for both ML (linear regression: $R^2 = 0.934$, $\beta = -0.967$, $p = 0.007$) and PW (linear regression: $R^2 = 0.559$, $\beta = -0.748$, $p = 0.008$) (Fig. 3). In the case of ML, we began our observations in the 8th week of pup age, and suckling dropped down to 0 in the 11th week. In case of PW, suckling dropped to 0 in the 7th and 8th weeks, but increased again in the 9th week, only to stop completely in the 10th week. Thus, the period of 7–11 weeks of age can be considered to be the weaning period. In this period, all the events of suckling were initiated by the pups, and the mother refused several suckling attempts (0.30 ± 0.24 refusals/h). There was no bias in the rate at which active parental care was provided to the pups by both the mothers (Mann–Whitney U test: ML: $U = 21.00$, $df = 5, 5$, $p = 0.095$; PW: $U = 19.50$ $df = 6, 6$, $p = 0.937$).

Alloparental care

An alloparent is an individual, other than the genetic parent, that provides care for conspecific young (Wilson 1975), and alloparental care is the investment of resources toward the survival of that conspecific young (Hamilton

Fig. 3 The rate of suckling by the two mothers at different ages (in weeks) of their pups. The suckling rates of ML are denoted by *closed diamonds* and those of PW are denoted by *open circles*. The *dotted line* shows the regression line for the suckling rates of ML, while the *dashed line* shows the regression line for PW
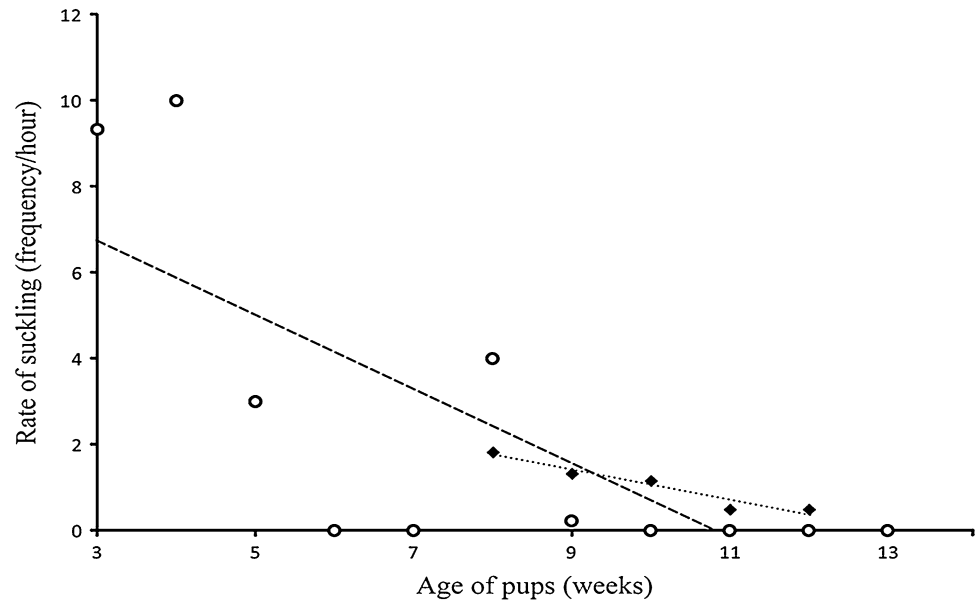
1964). Behaviours like suckling, allogrooming, providing regurgitated food material, playing and protecting pups by an adult towards pups other than their own were considered as alloparental care. ML provided alloparental care to the two pups of her daughter (PW) in the second year, when she did not give birth to a litter herself. Here, we designate her as ML_G (ML grandmother) for convenience. She showed all the behaviours included in the category of parental care, both active and passive, other than suckling, towards her grandpups.

Unlike in the case of parental care, the proportion of time spent in active alloparental care by ML_G did not decline significantly over the weeks (linear regression: $R^2 = 0.005$, $\beta = 0.074$, $p = 0.829$). She did not show any bias towards any of her grandpups, caring equally for both (Mann–Whitney U test: $U = 24.000$, $df = 6, 6$, $p = 0.39$). Though we observed considerable levels of alloparental care by ML_G, the total alloparental care was significantly less than the total parental care provided by PW and ML to their respective pups (Table 2). Though ML was pseudo-pregnant in the second year, she did not lactate, and hence we did not record any event of allosuckling by her. So, we re-calculated the parental care provided by herself and her daughter in the two seasons by removing suckling from the data. Even then, the care provided by ML_G was lower than the parental care provided by ML and PW (Table 2).

The time spent with pups was comparable between the three cases under study, namely, parental care by ML and PW, and alloparental care by ML_G (Mann–Whitney U test: $p > 0.05$). Of the time spent with the pups, that spent in guarding did not differ between the three cases (Mann–Whitney U test: $p > 0.05$). However, in the case of ML_G, the effort she put in guarding was significantly higher than

Table 2 Test statistics for all possible pairwise comparisons between the levels of parental care shown by ML and PW in the two seasons and alloparental care shown by ML_G using Mann–Whitney U test

Comparisons	U	df	p value
PC: ML vs. PW	13.000	5	1.00
ML: PC vs. APC	**25.000**	**5**	**0.008**
ML: (PC-CK) vs. APC	**25.000**	**5**	**0.008**
ML: APC vs. PW: PC	**98.500**	**11**	**0.010**
ML: APC vs. PW: (PC-CK)	**97.500**	**11**	**0.010**
(PC-CK) ML vs. PW	15.000	5	0.690

The statistically significant sets are given in bold

PC active parental care, *APC* Alloparental care, *CK* suckling

that she put into other active parental care behaviours (Wilcoxon paired-sample test: $T = 0.00$, $n = 11$, $p = 0.008$). There was no such difference observed in the distribution of parental behaviour of ML and PW. ML_G seemed to spend significantly higher amounts of her time with the pups in the presence of PW than expected by chance alone (Chi squared test: Chi square $= 70.026$, $df = 1$, $p < 0.001$) (Fig. 4).

Discussion

Alloparental care is thought to be energetically costly for the alloparent, but even so this apparently altruistic behaviour has been observed in 150 avian and 120 mammalian species (Riedman 1982). Most of the alloparenting cases are reported in animals where individuals live in stable social groups and breed either communally or
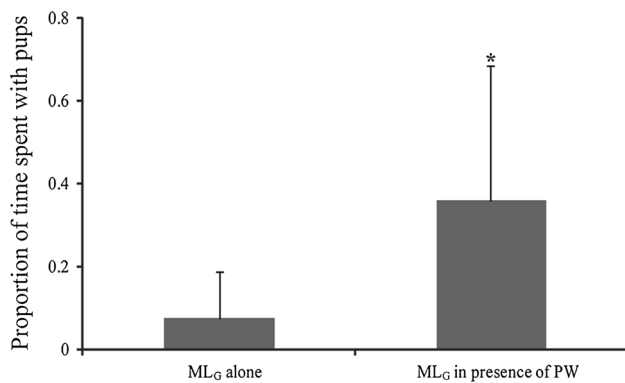
Fig. 4 Mean and standard deviation of the proportion of time spent with her grand-pups by ML_G alone and in the presence of her daughter PW. The *asterisk* denotes a statistically significant difference between the two

cooperatively (Emlen 1982; Solomon and French 1997). However, alloparental care has also been documented in some birds, mammals and fishes, where there is no ongoing social interaction between the true parent and the alloparent (Rohwer et al. 1999; Wisenden 1999).

Alloparenting behaviour is pronounced among social canids like grey wolves (Fox 1975; Allen 1979; Murie 1985), coyotes (Kleiman 1968; Gier 1975; Bekoff 1977; Bekoff and Wells 1980) and African wild dogs (Kühme 1965; Lawick and Lawick-Goodall 1971; Bekoff 1975), which are cooperatively breeding species, forming large hunting packs (Ewer 1973; Jennions and Macdonald 1994; Clutton-Brock 2006). In less social canids like golden jackals (*Canis aureus*) and silver-backed jackals (*Canis mesomelas*), juveniles frequently remain with their parents and provide care to the next litter (Lawick and Lawick-Goodall 1971; Moehlman 1979; Montgomerie 1981). In all these species, there are distinct categories of dominant and subordinates among which only the dominant pair can breed, while exerting reproductive suppression on non-breeding subordinates (Creel and Macdonald 1995; Moehlman and Hofer 1997).

Dogs are thought to have descended from pack-living wolves (Scott and Fuller 1965; Beck 1975; Kleiman and Brady 1978; Daniels 1983; Font 1987). Unlike in the other cooperatively breeding canids, in the free-ranging dogs, every individual in a group has an equal chance to breed and the breeding system is polygamous and polyandrous (Pal 2011). Though the dogs live in social groups, the group compositions are quite dynamic, driven by mating interests and resources (Sen Majumder et al. 2013). Parental care is present in the early stages of development, and the juveniles continue to stay with the mother even beyond weaning (Pal et al. 1998; Pal 2005). Since all adults (and sometimes even sub-adults) in a group mate, multiple females within a group often give birth at the same time.

To the best of our knowledge, this study is the first scientific observation of alloparental care in a natural dog group. Our focal group consisted of a family unit, and, in the second denning season, there were two females that mated, though only one became pregnant and gave birth. We observed parental care shown by the mother (PW) and alloparental care by the grandmother (ML_G) for both the pups. Though the levels of care provided by the grandmother were lower than that provided by the mother, both the bitches showed comparable levels of parental care towards their own brood in the two seasons. Thus, the lower levels of care that the grandmother provided to her daughter's brood (correcting for suckling) cannot be attributed to her incapability of providing more care. In fact, when we considered the time spent with pups when not showing parental care as a measure of the protection provided by the adult, the grandmother was seen to provide significantly more protection than other kinds of care, though both the females spent comparable amounts of time with the pups in the three scenarios. Since PW and ML_G were present with the pups simultaneously the majority of the times, the protection provided by ML_G was in addition to that provided by PW, and thus supplementary to PW's care. Since the two mothers (ML and PW) put in equal efforts in parental care, the pups in the second season received more care than those in the first, as ML_G added to the care provided by PW, very much like helpers in other species (Moehlman 1979; Johnson and Angeles 1980; Redondo et al. 1995).

Pseudopregnancy or pseudocyesis is quite common in domestic bitches that do not become pregnant during their oestrous. Pseudopregnancy in dogs typically has two phases, the growth phase and the lactation phase (Weber 1944). Prolactin levels are known to be higher than normal in pseudopregnant bitches, and this might be primarily responsible for lactation (Bastan et al. 1998; Gobello et al. 2001a, b). In the case of ML, we observed signs of pseudopregnancy prior to the birth of PW's pups, and it is possible that the absence of suckling did not allow prolonged lactation in ML, and hence we never observed allosuckling in the second season.

The presence of alloparental care in groups can be an evolutionary baggage that the dogs carry, reminiscent of their cooperatively breeding ancestry. However, since there is no reproductive dominance known in the dogs, the alloparental care observed is more similar to that observed in group-living primates including humans (Johnson and Angeles 1980; Jones 1981; Small 1990; Quinlan and Quinlan 2008; Md-Zain 2011; Morris 2011). Though we report here the first field observation of alloparental care made by us in detail, we have at least three other opportunistic observations in natural dog groups, for which we lack detailed behavioural data. It is thus not a rare

phenomenon in free-ranging dogs, and needs to be better understood. Dog groups often undergo fission and fusion, and so exclusive family groups are not expected to be common. Long-term observations with detailed pedigrees would be required to understand if alloparental care is only directed towards kin, as in the case of cooperatively breeding canids (Emlen 1982; Riedman 1982; Cornwallis et al. 2010; Lukas and Clutton-Brock 2012).

These dogs mostly depend on garbage and human charity for survival, and hence their resources are scanty and dispersed. This is probably why large groups are not formed, and foraging is often a solitary activity (Sen Majumder et al. 2013). Having multiple litters in a group increases competition, and such competition can be resolved both by infanticide and cooperative brood care. We have observed lactating bitches killing the pups of other bitches (Paul and Bhadra, unpublished) and allo-parental care towards related pups in a group within the same population of free-ranging dogs. Hence, the breeding system is quite diverse, and this adds to the plasticity of the social organization of the dogs (Sen Majumder et al. 2013).

References

Achappa A (2012) Stray dog chasing black buck. Conservation India Gallery July 27. http://www.conservationindia.org/gallery/stray-dog-chasing-blackbucks

Allen D (1979) Wolves of Minong: Isle Royale's wild community. University of Michigan Press, Ann Arbor

Allen W (1986) Pseudopregnancy in the bitch: the current view on aetiology and treatment. J Small Anim Pract 27:419–424

Bastan A, Findik M, Aslan S (1998) The use of cabergoline for treatment of pseudopregnancy in dogs with the purpose of suppressing lactation. Reprod Dom Anim 33:49–53

Beck A (1975) The ecology of "feral" and free-roving dogs in Baltimore. In: Fox MW (ed) The wild canids: their systematics, behavioral ecology and evolution. Van Nostrand Reinhold, Florence, pp 380–390

Bekoff M (1975) Social behavior and ecology of the African Canidae: a review. In: Fox MW (ed) The wild canids: their systematics, behavioral ecology and evolution. Van Nostrand Reinhold, Florence, pp 120–142

Bekoff M (1977) *Canis latrans*. Mamm Species 79:1–9

Bekoff M, Wells M (1980) The social ecology of coyotes. Sci Am 242:130–148

Berman M, Dunbar I (1983) The social behaviour of free-ranging suburban dogs. Appl Anim Ethol 10:5–17

Clutton-Brock T (1991) The evolution of parental care. Princeton University Press, New Jersey

Clutton-Brock J (1995) Origins of the dog: domestication and early history. In: Serpell J (ed) The domestic dog, its evolution, behaviour and interactions with people. Cambridge University Press, Cambridge, pp 7–20

Clutton-Brock TH (2006) Cooperative breeding in mammals. In: Kappeler PM, Schaik CP (eds) Cooperation in primates and humans. Springer, Berlin, pp 173–190. doi:10.1007/3-540-28277-7_10

Cornwallis CK, West SA, Davis KE, Griffin AS (2010) Promiscuity and the evolutionary transition to complex societies. Nature 466:969–972. doi:10.1038/nature09335

Creel S, Macdonald D (1995) Sociality, group size, and reproductive suppression among carnivores. Adv Study Behav 24:203–257

Daniels T (1983) The social organization of free-ranging urban dogs. I. Non-estrous social behavior. Appl Anim Ethol 10:341–363

Dewey K (1997) Energy and protein requirements during lactation. Annu Rev Nutr 17:19–36

Dewey K (1998) Effects of maternal caloric restriction and exercise during lactation. J Nutr 128:386S–389S

Emlen ST (1982) The evolution of helping. I. An ecological constraints model. Am Nat 119:29–39

Estes R, Goddard J (1967) Prey selection and hunting behavior of the African wild dog. J Wildl Manag 31(1):52–70

Ewer R (1973) The carnivores. Cornell University Press, USA

Font E (1987) Spacing and social organization: urban stray dogs revisited. Appl Anim Behav Sci 17:319–328

Fox M (1975) Evolution of social behavior in canids. In: Fox MW (ed) The wild canids: their systematics, behavioral ecology and evolution. Van Nostrand Reinhold, Florence, pp 429–460

Fox M, Beck A, Blackman E (1975) Behavior and ecology of a small group of urban dogs (*Canis familiaris*). Appl Anim Ethol 1:119–137

Gier H (1975) Ecology and behavior of the coyote (*Canis latrans*). In: Fox MW (ed) The wild canids: their systematics, behavioral ecology and evolution. Van Nostrand Reinhold, Florence, pp 247–262

Gobello C, Baschar H, Castex G, de la Sota RL, Goya RG (2001a) Dioestrous ovariectomy: a model to study the role of progesterone in the onset of canine pseudopregnancy. J Reprod Fertil 57:55–60

Gobello C, Concannon PW, Iii JV (2001b) Canine pseudopregnancy: a review. In: Concannon PW, England G, Verstegen III J, Linde-Forsberg C (eds) Recent advances in small animal reproduction. International Veterinary Information Service, Ithaca, NY, A1215.0801

Gubernick DJ (1981) Parent and infant attachment in mammals. In: Gubernick DJ, Klopfer PH (eds) Parental care in mammals. Springer, New York, pp 243–305

Hamilton W (1964) The genetical evolution of social behaviour. II. J Theor Biol 7:17–52

Jennions M, Macdonald D (1994) Cooperative breeding in mammals. Trends Ecol Evol 9:89–93

Johnson C, Angeles L (1980) Alloparental care and kinship in captive social groups of vervet monkeys (*Cercopithecus aethiops sabaeus*). Primates 21:406–415

Jones CB (1981) Comment on "Allomothering Langurs" in Hanuman. Ethol Sociobiol 2:89–90

Kaushik A (2008) Dogs hunt black bucks at Velavadar sanctuary. The Times of India, September 17

Kleiman D (1968) Reproduction in the Canidae. Int Zoo Yearb 8:3–8

Kleiman DG (2011) Canid mating systems, social behavior, parental care and ontogeny: are they flexible? Behav Genet 41:803–809. doi:10.1007/s10519-011-9459-0

Kleiman D, Brady C (1978) Coyote behavior in the context of recent canid research. In: Bekoff M (ed) Coyotes: biology, behaviour and management. Academic, New York, pp 163–188

Kleiman D, Malcolm J (1981) The evolution of male parental investment in mammals. In: Gubernick DJ, Klopfer PH (eds) Parental care in mammals. Springer, New York, pp 347–387

Kruuk H (1975) Functional aspects of social hunting by carnivores. In: Baerends G, Beer C, Manning A (eds) Functions and evolution in behaviour: essays in honour of Professor Niko Tinbergen. Oxford University Press, Oxford

Kühme W (1965) Communal food distribution and division of labour in African hunting dogs. Nature 205:443

Lukas D, Clutton-Brock T (2012) Cooperative breeding and monogamy in mammalian societies. Proc R Soc Lond B 279:2151–2156. doi:10.1098/rspb.2011.2468

Macdonald D (1979) The flexible social system of the golden jackal, *Canis aureus*. Behav Ecol Sociobiol 5:17–38

Macdonald D (1983) The ecology of carnivore social behaviour. Nature 301:379–384

Md-Zain BMCEC, Ch'ng CE (2011) The activity patterns of a group of Cantor's dusky leaf monkeys (*Trachypithecus obscurus halonifer*). Int J Zool Res 7:59–67

Mech LD (1970) The wolf: ecology and behavior of an endangered species. Natural History Press, Garden City

Moehlman PD (1979) Jackal helpers and pup survival. Nature 277:382–383

Moehlman P, Hofer H (1997) Cooperative breeding, reproductive suppression, and body mass in canids. In: Moehlman PD, Hofer H, Solomon NG (eds) Cooperative breeding in mammals. Cambridge University Press, Cambridge, pp 76–128

Montgomerie R (1981) Why do jackals help their parents? Nature 289:824–825

Morris C (2011) Exploring the necessity of others in human evolution. J Soc Evol Cult Psychol 5(4):293–295

Murie A (1985) The wolves of Mount McKinley. University of Washington Press, Seattle

Oppili P (2013) Birds fall prey to dogs at Pallikaranai. The Hindu, October 29

Pal SK (2005) Parental care in free-ranging dogs, *Canis familiaris*. Appl Anim Behav Sci 90:31–47. doi:10.1016/j.applanim.2004.08.002

Pal S (2008) Maturation and development of social behaviour during early ontogeny in free-ranging dog puppies in West Bengal, India. Appl Anim Behav Sci 111:95–107. doi:10.1016/j.applanim.2007.05.016

Pal SK (2011) Mating system of free-ranging dogs (*Canis familiaris*). Int J Zool 2011:1–10. doi:10.1155/2011/314216

Pal S, Ghosh B, Roy S (1998) Dispersal behaviour of free-ranging dogs (*Canis familiaris*) in relation to age, sex, season and dispersal distance. Appl Anim Behav Sci 61:123–132

Peterson R, Ciucci P (2003) The wolf as a carnivore. In: Mech LD, Boitani L (eds) Wolves: behavior, ecology, and conservation. University of Chicago Press, Chicago, pp 104–130

Quinlan RJ, Quinlan MB (2008) Human lactation, pair-bonds, and alloparents. Hum Nat 19:87–102. doi:10.1007/s12110-007-9026-9

Redondo T, Tortosa FS, Reyna LA (1995) Nest switching and alloparental care in colonial white storks. Anim Behav 49:1097–1110

Rheingold H (1963) Maternal behavior in mammals. Wiley, New York

Riedman ML (1982) The evolution of alloparental care and adoption in mammals and birds. Q Rev Biol 57:405–435

Rogowitz G (1996) Trade-offs in energy allocation during lactation. Am Zool 36:197–204

Rohwer S, Herron J, Daly M (1999) Stepparental behavior as mating effort in birds and other animals. Evol Hum Behav 20:367–390

Sandell M (1989) The mating tactics and spacing patterns of solitary carnivores. In: Gittleman JL (ed) Carnivore behaviour, ecology and evolution, vol I. Cornell University Press, Ithaca, pp 164–182

Scott J, Fuller J (1965) Genetics and the social behavior of the dog. University of Chicago Press, Chicago

Scott J, Marston M (1950) Critical periods affecting the development of normal and mal-adjustive social behavior of puppies. Pedagog Semin J Genet Psychol 77:25–60

Sen Majumder S, Bhadra A, Ghosh A et al. (2013/2014) To be or not to be social: foraging associations of free-ranging dogs in an urban ecosystem. Acta Ethol 17(1):1–8. doi:10.1007/s10211-013-0158-0

Serpell J (1995) The domestic dog: its evolution, behaviour and interactions with people. Cambridge University Press, Cambridge

Sillero-Zubiri C, Hoffmann M, Macdonald DW (2004) Canids: foxes, wolves, jackals, and dogs: status survey and conservation action plan. Information Press, Oxford

Small MF (1990) Alloparental behaviour in Barbary macaques, *Macaca sylvanus*. Anim Behav 39:297–306

Solomon N, French J (1997) Cooperative breeding in mammals. Cambridge University Press, Cambridge

van Lawick H, van Lawick-Goodall J (1971) Innocent killers. Houghton Mifflin, Boston

Vanak A, Gompper M (2009) Dietary niche separation between sympatric free-ranging domestic dogs and Indian foxes in central India. J Mamm 90:1058–1065

Vanak AT, Thaker M, Gompper ME (2009) Experimental examination of behavioural interactions between free-ranging wild and domestic canids. Behav Ecol Sociobiol 64:279–287. doi:10.1007/s00265-009-0845-z

Weber AF (1944) Pseudopregnancy in dogs. Iowa State University Vet 7(1):32–38

Welker W (1959) Genesis of exploratory and play behavior in infant raccoons. Psychol Rep 5(3):764

Wilson EO (1975) *Leptothorax duloticus* and the beginnings of slavery in ants. Evolution 29(1):108–119

Wisenden B (1999) Alloparental care in fishes. Rev Fish Biol Fish 9:45–70

Woodroffe R, Vincent A (1994) Mother's little helpers: patterns of male care in mammals. Trends Ecol Evol 9:294–297