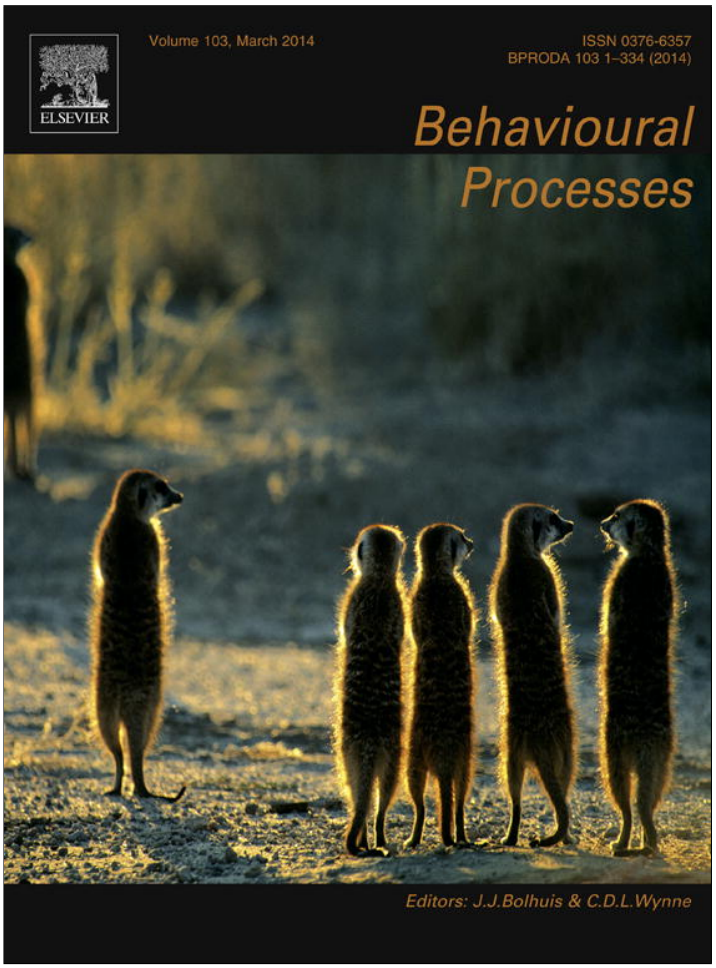

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Selfish mothers? An empirical test of parent-offspring conflict over extended parental care

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ABSTRACT

Parent-offspring conflict (POC) theory is an interesting conceptual framework for understanding the dynamics of parental care. However, this theory is not easy to test empirically, as exact measures of parental investment in an experimental set-up are difficult to obtain. We have used free-ranging dogs *Canis familiaris* in India, to study POC in the context of extended parental care. We observed females and their pups in their natural habitat for the mother's tendency to share food given by humans with her pups in the weaning and post-weaning stages. Since these dogs are scavengers, and depend largely on human provided food for their sustenance, voluntary sharing of food by the mother with her pups is a good surrogate for extended parental care. Our behavioural observations convincingly demonstrate an increase of conflict and decrease of cooperation by the mother with her offspring over given food within a span of 4–6 weeks. We also demonstrate that the competition among the pups in a litter scales with litter size, an indicator of sib–sib competition.

1. Introduction

Parental care is an indispensible part of development in mammalian species, where mothers suckle their offspring. The offspring often continue to stay with the mother after weaning and the mother continues to share food and shelter with them. Most mothers do not extend care towards their offspring for indefinite periods, and at some time after weaning the offspring become independent of the mother. Parent-offspring conflict theory predicts that the mother would try to wean her offspring a little earlier than the offspring would be ready to wean themselves, thereby entering the zone of conflict with them for a short span of time (Trivers, 1974). Though the theory was originally formulated in the context of weaning, it is also relevant in other contexts where a parent and his/her offspring have conflicting interests. Conflict has been reported in various contexts from diverse species like horses, arctic wolves, chimpanzees, budgerigars, tits, etc. (Horvat and Kraemer, 1982; Duncan et al., 1984; Stamps et al., 1985; Packard et al., 1992; van Dijk et al., 2012).

There are several theoretical models that address POC in different contexts like reproduction, intra-brood competition, resource allocation and parental favouritism towards particular offspring (Macnair and Parker, 1978; Mock and Parker, 1997; Lessells, 2002; Parker et al., 2002; Shizuka and Lyon, 2013). Though relatedness between parents, offspring and siblings can be measured easily, it is nearly impossible to measure precisely parental investment and the costs and benefits to the concerned parties in nature. In some studies attempts have been made to quantify parental care in terms of milk ingested by offspring, sometimes as a correlate of weight gain by the individual pups, and sometimes by the duration of suckling (Gomendio, 1991; Godfray and Parker, 1992; Ahlstrøm and Wamberg, 2000; Riek, 2008; Pluháček et al., 2010). However there is considerable variation in the suckling rates of individual pups and in hunger levels of individuals; hence such measures can only provide a rough estimate of parental investment (Cameron, 1998; Cameron et al., 1999). It is therefore not surprising that empirical tests of the theory in nature are sparse, especially in the original context of weaning. Due to these limitations to measuring parental investment, POC theory has been claimed to be one of the most contentious subjects in behavioural and evolutionary ecology and also one of the most recalcitrant to experimental investigation (Alexander, 1974; Clutton-Brock, 1991). In this paper we report the results of an experiment that we carried out to test the presence of parent-offspring conflict in a mammalian system over extended parental care in the field using free-ranging dogs as a model system.

Free-ranging dogs are an integral part of the urban ecology in many countries. In India, dogs have lived outside of human homes for centuries, and have also been used for hunting, but it is interesting to note that they have not undergone the usual domestication process to become exclusively pets as in most developed countries. The free-ranging dogs in India live in small groups or singly on

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streets (Sen Majumder et al., 2013) and depend on garbage and human generosity for their sustenance (Pal, 2001). Competition over food is quite high, and fights are very common at garbage dumps near roadside food stalls, or when humans occasionally offer a piece of food to the dogs (Das and Bhadra, in preparation).

These dogs are an excellent model system for addressing POC. They breed twice a year, once in the autumn and once in the spring, but a given female usually produces one litter per year (Pal, 2003; Paul et al., in preparation). The mother typically spends most of her time with the pups in the early weeks, and only moves out of her shelter to feed for short periods. Her absence increases when the pups gain mobility (Paul et al., in preparation). Weaning in dogs generally begins when the pups are about 6 weeks old. At this stage the mother begins to refuse to feed the pups while they continue to demand suckling (Malm and Jensen, 1997). The free-ranging pups begin to eat solid food from around 5 weeks, when the mother gives them regurgitated food and at times hunts small prey to feed her pups, though the mothers continue to suckle up to 10–11 weeks (Pal, 2005, 2008). Often mothers with litters are fed by humans and the pups share this food with their mother when they begin to feed on solids (Paul et al., in preparation). We observed that the mother begins to refuse sharing of such food with her pups soon after weaning and the competition between them and the mother seems to increase over the weeks. Since it is extremely difficult to measure parental investment in terms of the actual amount of milk that a pup receives or the energy that the mother spends in caring for her pups, we used the mother's tendency to share food with her pups as a surrogate for extended parental care. This is especially relevant in these dogs because they are scavengers, and they often beg for food from humans. Competition over food is high, and most of the agonistic interactions within and between dog groups take place at feeding sites (Pal et al., 1998). Using the surrogate behaviour of food sharing by the mother for our observations, we carried out a field experiment to examine whether post-weaning conflict over food exists between the mother and her pups in the Indian free-ranging dogs. We predict that during the early stages of weaning the mother should be ready to share food given by humans with her pups, but as the pups are weaned, the mother should gradually reduce her tendency to share food with them, leading to competition over given food between her and the pups in her litter.

2. Methods

The experiment was performed on mother-litter groups of free-ranging dogs in Kolkata (22°34′ N, 88°24′ E) and at the IISER-K campus at Mohanpur (22°94′ N, 88°53′ E), West Bengal, India in two consecutive years. We collected data on 8 litters in the first year (January–April 2011) and 7 litters in the second year (December 2011–April 2012). The experiments commenced when the pups were 8–11 weeks old, and at least one act of refusal to suckle by the mother had been observed. Each litter was observed for a minimum of four and a maximum of six weeks, and only the groups where the mother and at least one pup survived through this period were used for the analysis. Thus we obtained data on 15 mothers and their litters varying in size from one to seven pups (please see Electronic Supplementary Material (ESM) Table 1 for details).

The experiment was conducted in two sessions, morning (between 1000 and 1230 h) and evening (between 1530 and 1700 h), on three consecutive days of a week for all litters, thus yielding a total of 430 observation sessions. The mother and her pups were offered pieces of bread and biscuits in the week before the actual experiment and their preference for either were noted. Some groups were choosy about a particular type of food, while others ate either type of food. We decided to give them either bread or biscuits because they are likely to find these in their day to day foraging at garbage bins and at roadside food joints as people typically feed the dogs with bread or biscuits in response to begging. Hence it would be natural for them (or at least the mother) to receive pieces of bread or biscuits from the experimenter, without causing alarm.

The experiment consisted of giving pieces of bread or biscuits to the mother-litter groups, and recording the response of the individuals to the food. Bread was used for only those groups that showed a clear preference for bread over biscuits in the preliminary trials. The type of food given was kept constant throughout the experiment for a group. The experimenter offered a piece of food to the group of dogs and waited until it was completely consumed before offering the next piece (please see ESM Fig. 1). The number of offerings made during a session was equal to the number of individuals present in the group at the time of the experiment. The entire experiment was video recorded and the videos were used to tabulate the data at the end of the experiment. For each piece of food offered, we recorded which individual ate the piece, the latency to first reaction (FR), time taken to eat the piece (ET) and the interactions between the mother and pups. The proportion of food taken by an individual was calculated by dividing the number of pieces eaten by the individual by the total number of pieces of food given to the group in a week. For each piece of given food, we recorded the behaviour shown by the mother.

Typically the pups always showed interest in the food item, and only the mother's behaviour showed considerable variation between sessions. We used the mother's behaviour towards the pups to define cooperation and conflict. We recorded seven distinct behaviours that the mother showed towards the pups as a response to the giving of food (please see videos in ESM for details).

Disinterest (DI): The mother did not make an attempt to reach the food, or looked away from it.
Allow (AL): The mother looked at the food, but did not move to grab it, allowing the pups to take it.
Offer (OF): The mother took the food and then gave it to the pups, without eating it herself.
Share (SH): The mother took the food and shared it with the pups, and did not show any aggression.
Compete for food (CF): The mother and pups both tried to grab the food and whoever got to the food first took it, without showing any aggression towards the others.
Compete aggressively (CA): The mother barked at or attacked the pups if they tried to get the food, and took the food herself.
Snatch (SN): The mother snatched the food away from the pups and ate it herself.

We used a qualitative assessment method to give scores to the mothers for the status of their health during the experiment. From the videos, each mother was scored on the first day of observation in a week, for each week of observations. The scores were given on body size (small, medium, large), condition of fur (poor, medium, good), nutritional status (poor, medium, good) and disease (present, absent). These qualitative scores were then converted to numerical scores, such that the highest score a bitch could get was 10 (large – 3; good fur – 3; well fed – 3, no disease – 1). However, since the body size was constant for all females throughout the experiment, we removed this factor from the body condition index, and gave each bitch a score out of 7 for every week of the experiment (see ESM Table 2 for details).

3. Data analysis and statistics

We scored the number of suckling attempts made by the pups and the number of times the mother rejected suckling solicitations from the videos for each week of the experiment. The data on total suckling solicitations per week was transformed using

a Box–Cox transformation and subjected to a generalized linear mixed model (GLMM) analysis, which incorporates both fixed and random effects, to check if the suckling attempts made by the pups decreased with age, signifying weaning. The number of suckling attempts was fed as the dependent variable, while the age of the pups, litter size and mother's body condition were continuous predictors. The identity of the mother was incorporated as a random factor in the overparameterized model.

We pooled all instances of disinterest, allow, offer and share into the category of cooperation and all instances of compete, compete aggressively and snatch into the category of conflict for our analysis. We estimated the amount of conflict in a week by counting the number of pieces for which the mother showed conflict and divided this by the total number of pieces given to the group. If two individuals shared a piece, each was given a score of 0.5. The proportion of cooperation and conflict in a week added up to 1. The time taken by the individuals to react to the giving of the food was estimated from the videos and labelled as the latency to first reaction (FR), and the time taken by them to finish a piece of food was labelled as the eating time (ET). The FR and ET were computed for all instances of giving food. The data on conflict did not fit any known distribution, and hence was transformed to a normal distribution using Box–Cox transformation. We used a generalized linear mixed-effects model (GLMM) to examine how conflict shown by the mother might depend on litter size, age of the pups (in weeks) and her body condition. In the model we also incorporated the ET and FR as factors that might depend on conflict levels. We expected the levels of cooperation to decrease and conflict to increase with pup age and litter size. Mother's identity ($N = 15$) was incorporated as a random variable, rather than fixed factor, in order to prevent pseudo-replication.

The number of pieces eaten by an individual was counted for each week. We pooled the data for the pups in a litter to compute the mean proportion of food taken by the pups, and designated this as the average pup. The pup that took the maximum amount of food in a litter was designated as the max pup for that litter. The amount of food eaten by the mother and max pup in a group were then subjected to a repeated measures analysis of variance, where mothers and pups were considered as subjects. A similar repeated measures ANOVA was performed for a subset of the data considering the amount of food eaten only in the cases of conflict. The data on the body condition of the mothers was subjected to repeated measures ANOVA.

Data analysis was carried out using in StatistiXL version 1.8 and STATISTICA version 10.0.

4. Ethical note

Our experiments were conducted in the natural habitat of the dogs, without causing any alarm to the mothers or the pups. The food used for the experiment was of a known type, and was not potentially harmful to the dogs. No invasive techniques were used for the experiments, and the observer recorded the experiment using a small handheld camera as the pups often get alarmed by tripods in close proximity to them. In India, free-ranging dogs are fed by humans quite routinely, and we did not need to obtain permission for this experiment.

5. Results

The mothers showed significant variation in their body condition across the entire period of the experiment (repeated measures ANOVA; Wilks' $\lambda = 0.023$, $F_{6,9} = 65.151$, $p < 0.0001$; ESM Fig. 2). However, there was no significant variation in the body condition of different mothers at the same stage of the experiment, i.e. between subject effects in the repeated measures ANOVA were not significant ($F_{14,90} = 1.382$, $p = 0.178$; Fig. 1).

Suckling solicitations by pups over weeks were transformed using a Box–Cox transformation ($\lambda = -0.8879$; mean $\pm$ s.d. $= 0.3226 \pm 0.4484$). Suckling attempts reduced significantly with pup age (GLMM: $F_{1,68} = 15.47$, $p < 0.001$), and were independent of the size of the litter to which the pup belonged and the mother's body condition (Table 1). Using the original data, we calculated the predicted values for suckling attempts and plotted them with the observed ones (Fig. 2). For the normalized data, the predicted and observed values overlapped completely. The observed reduction in solicitation of suckling by the pups is indeed more drastic than the predicted values, as evident from Fig. 2. Thus the pups indeed weaned during the early part of this experiment, and conflict if any can be rightly considered as post-weaning conflict.

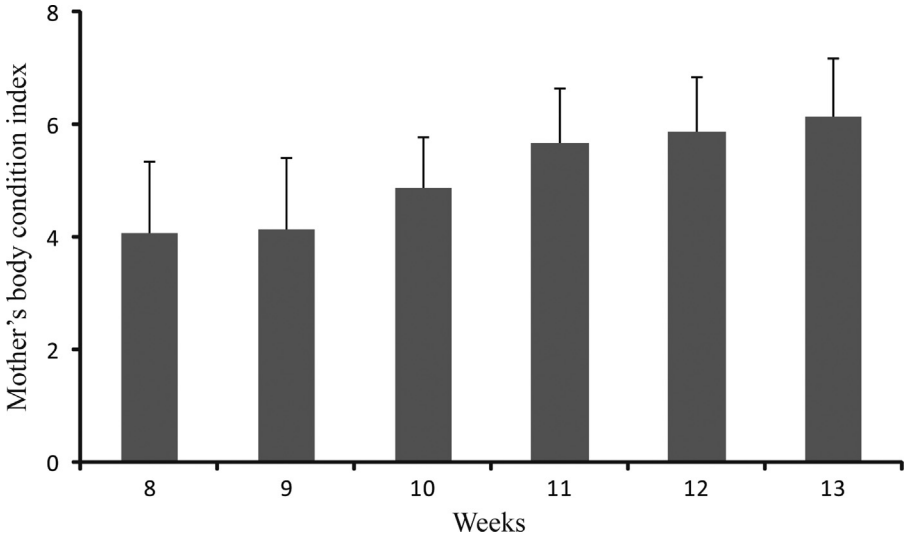

Fig. 1. Mean and standard deviation of the body condition index (BCI) of the mothers ($N = 15$) at different weeks of pup age, estimated from the videos during the entire span of the experiment for each group. There was significant improvement in BCI over time for individual mothers (repeated measures ANOVA, Wilks' $\lambda = 0.023$, $F_{6,9} = 65.151$, $p < 0.0001$).

Table 1
GLMM results for the effect of age of pups, litter size and mother's body condition on the suckling attempts by pups. Over-parameterized model after Box–Cox transformation of data (λ = −0.8879; mean ± s.d. = 0.3226 ± 0.4484).

	$\beta \pm$ S.E.	T	p	95% CIs
Weeks	−0.6836 ± 0.1738	−3.9337	0.0002	−1.0304 to −0.3368
Litter size	0.2860 ± 0.8433	0.3392	0.7355	−1.3967 to 1.9687
Mother's body condition	0.1221 ± 0.2190	0.5576	0.5789	−0.3148 to 0.5590
Random effect				
Mother: estimated variance ± S.E. = 0.004549 ± 0.108666				

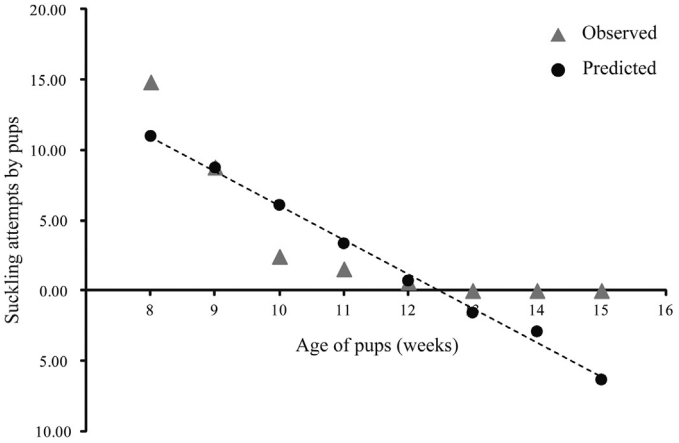

Fig. 2. Mean observed suckling solicitations by pups at different ages and the mean expected suckling attempts fitted by a generalized linear model. The observed drop in suckling with increase in pup age is significant, and this suggests that weaning indeed occurs around the 10th week.

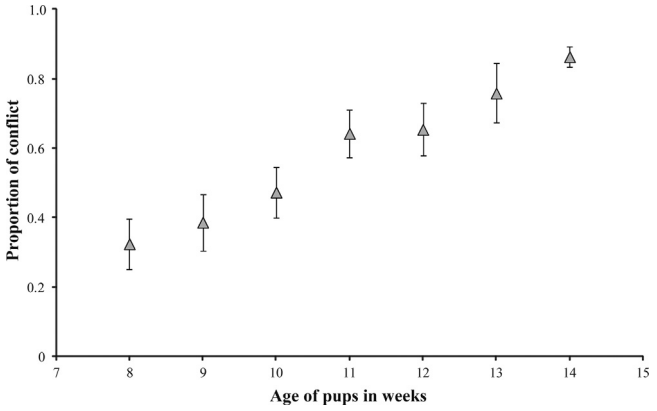

Fig. 3. Conflict exists: The mean and standard error of the proportion of conflict over pup age in weeks in free-ranging dogs, *Canis familiaris*.

We observed instances of conflict over food between the mother and pups in all 15 groups, though the level of conflict and the time of onset of conflict were quite variable across groups. Conflict over given food increased with pup age (GLMM: $F_{1,66}$: 13.8594, $p = 0.0004$) (Fig. 3), and was independent of litter size and the mother's body condition. The latency to first reaction (FR) did not depend significantly on the levels of conflict, though the eating time varied with conflict levels (GLMM: $F_{1,66}$: 7.9014, $p = 0.0065$). The random variable (identity of the mother) was significant in the model (variance = 18.4636, S.E. = 13.357, $p < 0.0001$). Table 2 gives the details of the GLMM performed for conflict.

The proportion of food taken by the mother did not depend on the size of her litter per se, as seen from the GLMM, though interaction terms involving litter size were significant in the model. The significant interaction between litter size and age of pups ($F_{1,74}$: 9.1560, $p = 0.0034$) suggests that as the pups grew older, the mothers with larger litters tended to show higher levels of conflict as

Table 2
Results from the GLMM for all effects for both conflict and cooperation. The identity of mothers was incorporated as a random variable in the models, while litter size and age of pups in weeks were fixed factors. The * denote statistically significant effect of a factor in the model.

	Estimate	S.E.	z	p
Conflict				
Intercept	−3.59453	0.78489	−4.580	4.66e−06***
Litter size	0.36009	0.18009	2.000	0.04555*
Weeks	0.23957	0.06658	3.598	0.00032**
Litter size: weeks	−0.02624	0.01510	−1.738	0.08221
Cooperation				
Intercept	1.60347	0.86698	1.849	0.06439
Litter size	−0.23365	0.22825	−1.024	0.30601
Weeks	−0.20212	0.07579	−2.667	0.00766**
Litter size: weeks	0.00717	0.02004	0.358	0.72044

compared to mothers with smaller litters. Similarly, there was significant interaction between the age of pups and the body condition of the mothers ($F_{1,74}$: 7.8415, $p = 0.0065$), suggesting that as the pups grew older, there was a significant improvement in the health of the mothers with the increase in their conflict levels. The strongly significant three-way interaction between litter size, age of pups and the mother's body condition ($F_{1,75}$: 22.3537, $p < 0.0001$) supports this conclusion (Table 3).

The amount of food eaten differed significantly across the weeks (repeated measures ANOVA: Wilks' λ = 0.575, $F_{5,24} = 3.541$, $p = 0.015$) for the pooled data, but was not significantly different over the weeks for only the cases of conflict (repeated measures ANOVA: Wilks' λ = 0.825, $F_{5,24} = 1.016$, $p = 0.430$). There was significant variation in the proportion of food eaten by the mothers and max pups for the total food given (repeated measures ANOVA, between subject effects: df = 1, $F_{1,28} = 11.264$, $p = 0.002$). However, when only the cases of conflict were considered, the mothers and max pups competed equally (repeated measures ANOVA, between subject effects: df = 1, $F_{1,28} = 0.014$, $p = 0.906$). Thus, though the pups ate most of the total food given in the entire span of the experiment (81.10 ± 12.84%, ESM Fig. 3), in situations of conflict, the mothers and pups ate comparable amounts of food, and thus could be considered to be competing earnestly.

6. Discussion

We have successfully demonstrated the presence of conflict between the mother and her offspring over extended parental care in the free-ranging dogs of India. Our results show that mothers begin to compete with their pups over food sharing during the weaning stage, and this competition increases significantly with pup age, thereby leading to a decrease in extended parental care (cooperation). Considering the proportion of food eaten by the pups and the mothers during the experiment we see that though the pups as a group eat most of the given food, in situations of conflict the mothers eat as much as the max pups, and hence comparable amounts, if not more, than an average pup. This result, coupled with the fact that the proportion of food the mother takes is independent of the size of her litter, suggests that the mother and her pups compete equally, and the pups get to eat more food on average

Table 3
GLMM results for the interaction of the levels of conflict shown by the mother with five different parameters tested. Over-parameterized model with type III decomposition after Box–Cox transformation of conflict data ($\lambda = 0.2635$; mean ± s.d. = 2.4823 ± 1.4880), with the identity of the mother treated as a random effect and all other parameters as fixed effects. Only the significant and relevant interaction terms in the model have been reported in the table.

	$\beta \pm$ S.E.	T	p	95% CIs
Weeks	−0.4545 ± 0.1220	−3.7228	0.0004	−0.6987 to −0.2107
Litter size	0.3012 ± 0.5726	0.5260	0.6006	−0.8420 to 1.4444
Mother's body condition (MBC)	−0.0144 ± 0.1504	−0.0959	0.9240	−0.3148 to 0.2850
Latency to first reaction (FR)	0.1565 ± 0.0896	1.7462	0.0854	−0.0224 to 0.3354
Eating time (ET)	−0.2680 ± 0.0953	−2.8109	0.0065	−0.4584 to −0.0776
Weeks * Litter size	−1.4868 ± 0.4913	−3.0259	0.0034	−2.4657 to −0.5077
Weeks * MBC	−0.4423 ± 0.1579	−2.8003	0.0065	−0.7571 to −0.1276
Litter size * FR	1.0976 ± 0.3487	−3.1475	0.0024	0.4028 to 1.7925
Litter size * MBC	0.9452 ± 0.4731	1.9979	0.04940	0.0025 to 1.8877
FR * ET	−0.5378 ± −0.2151	−2.5000	0.0146	−0.9664 to −0.1092
Weeks * Litter size * MBC	−0.9940 ± 0.1809	−5.4933	<0.0001	−1.3543 to −0.6340
Random effect				
Mother: estimated variance ± S.E. = 18.4636 ± 13.3573				

because of the cooperation that the mother otherwise shows. The significant decrease of the time taken to eat a piece of given food (ET) with increase in conflict also suggests that the competition is quite severe, which is corroborated by the fact that in situations of conflict, the mother and the max pup compete equally for food.

In the Indian free-ranging dogs competition over food is a reality, and we have observed mothers fight with their offspring over food. Mother dogs lose a lot of weight when they suckle pups (M. Paul, pers. comm.), and they have to compete with other dogs to obtain food in order to regain the energy to support their next litter. We have observed that people tend to give food to suckling mothers, but such supplies typically dwindle when the pups grow up and begin to fend for themselves. Our body condition indices show that the mothers indeed are at a poorer state of health when they are nearing the weaning period, possibly due to the toll that suckling takes on them, and their physical condition rapidly improves over the next few weeks (ESM Fig. 1). Moreover, though litter size and the mother's body condition did not influence the levels of conflict in the model, the interaction term did. This suggests that the mothers who had larger litters indeed tended to show more conflict when they had poorer body conditions at the beginning of the experiment. The mother has a short window of time when she can get food without fighting with other adults, and her only competition comes from her own offspring. A mother that shares food well beyond the weaning stage with her offspring is likely to lose the opportunity to quickly replenish her energy reserves for a litter in the next breeding season. The fact that all the mothers had comparable body indices at the end of the experiment and there was a significant increase in the body condition of mothers over time shows that they were indeed making good use of this window of time to regain their energy reserves. Hence the sharing of food provided by humans was a good surrogate for parental investment in our study system.

The steady decrease seen in the suckling solicitations by the pups suggest that the pups had indeed weaned in the 9–10 week window, and conflict over suckling, if any, would have been resolved. Hence whatever conflict we saw during our experiment pertained to extended parental care, and did not depend on the extent to which the mother was spending her energy in suckling her pups. In fact the maximum levels of conflict were seen in the last two weeks of the experiment, when no suckling refusals were seen, and the mothers were in an improved state of health.

Mother-offspring conflict over resource allocation begins as early as the neonatal stage; the dynamic relationship of foetal growth and development with the mother's physiological state is regulated by various hormonal and genetic mechanisms during gestation. These interactions between the mother and the foetus through the placenta are classic examples of neonatal POC (Vaughan et al., 2012; Fowden and Moore, 2012). During the initial stages after birth the mother typically extends parental care towards the offspring, and mother-offspring conflict becomes evident only during weaning through behaviours like increased suckling refusal (Pavé et al., 2010) and reduced response to begging by infants (Riou et al., 2012). Food sharing between parents and dependent offspring is known in many mammalian species like the hunting dog *Lycaonpictus* (Courchamp et al., 2002), gorillas (*Gorilla gorilla gorilla*) (Nowell and Fletcher, 2006), chimpanzees (*Pan troglodytes*) (Nishida and Turner, 1996), etc. Food transfer through regurgitation occurs in dogs and wolves (Malm, 1995; Pal, 2005; Mech et al., 1999) when the pups approach the weaning stage. Food sharing between the mother and offspring beyond weaning, though not very common, is known to occur in primates like chimpanzees and orangutans (*Pongo pygmaeus wurmbii*) (Silk, 1978; Jaeggi et al., 2008). Such kind of food transfer has been demonstrated to be used for information transfer, rather than for meeting the nutritional demands of the offspring, and is thus not relevant in the context of POC (Jaeggi et al., 2008). Due to the many ways in which a parent extends care to its offspring, the manifestations of POC can be very diverse. It has been shown to depend on environmental, social and cultural conditions in several species like vervet monkeys (*Cercopithecus aethiops*), collared peccaries (*Tayassu tajacu*), bighorn sheep (*Ovis canadensis*), white-tailed deer (*Odocoileus virginianus*), and even in some human societies (Hauser and Fairbanks, 1988; Babbitt and Packard, 1990; Berger, 1979; Therrien et al., 2008; Fouts et al., 2005). However, POC over extended parental care beyond weaning in a natural habitat has rarely been studied other than for humans.

In the free-ranging scavenging dogs food is a limiting resource, and the mother's conflict over food sharing with her pups during and after weaning is an example of the influence of the environment on the shaping of behaviour in group-living species. These dogs depend on humans for food, but are not taken care of like their domesticated brethren. Though parental care is typically considered to be beneficial to the offspring, in resource-limiting conditions, living with a caring mother might be detrimental to the long term survival of offspring, as has been demonstrated in the case of earwigs (*Forficula auricularia*) reared in food restricted conditions (Meunier and Kölliker, 2012). It has even been suggested that in mammals and birds mothers do not bear the cost of parental investment but shift it to their current and future progeny. Hence there is need to explore parental care and conflict from the perspective of both intra-generational as well as inter-generational trade-offs (Santos and Nakagawa, 2012). Our observations of the presence of conflict between the mother and her

pups over extended parental care in the free-ranging dogs opens up the possibility of using them as a model system for studying the interplay of ecological and social parameters that influence parent-offspring conflict and shape life history traits.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at http://dx.doi.org/10.1016/j.beproc.2013.10.006.

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