



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.

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1. Introduction

Parental care is an indispensable 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; Ahlström 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

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