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Do older siblings help raise their younger siblings? A case study of alloparental care in Indian free-ranging dogs

Tanima Choudhury

Abstract
In wolf packs alloparental care is predominately present. During the process of dog domestication the dogs have undergone certain behavioural changes. Due to shifting to a scavenging lifestyle from a hunting lifestyle the free-ranging dogs mainly live singly or in small groups rather than in large wolf like packs. Due to food scarcity the offsprings often move away from their parents. In places where sufficient food supply is present offsprings often stay with their mother and alloparental care of pups by close genetic relatives has been observed. In this study we observed the surviving offspring of the previous litter provide alloparental care to the pups of her mother's newest litter. Alloparental care was provided in the form of increased guarding, play and food sharing during the early weeks of pups' lives. The increased care of the pups by the alloparent could increase the pups' chances of surviving to adulthood.

Keywords: Alloparental care, inclusive fitness, Indian free-ranging dogs, older sibling

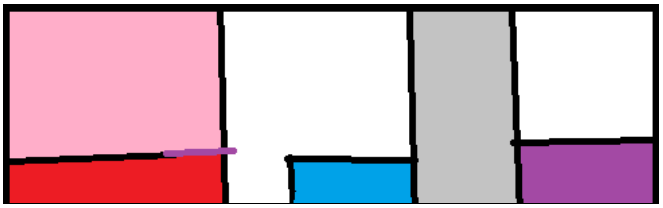
Introduction
The basic unit of wolf packs consists of the mated pair (dominant male and the dominant female), their previous offsprings and siblings of the mated pair. The wolves are monestrous and reproduce offsprings only once every year. The older offsprings remain within their natal pack for 10-54 months [1]. The wolf pack sometimes contain unrelated individuals (usually males 1-3yrs old) which have left or lost their natal packs and have joined a pack already containing a mated pair [2]. The young wolves mainly do not breed in their natal packs and help the breeding pair raise their offsprings by regurgitating food, guarding the wolf pups and teaching them how to hunt. So, alloparental care is quite prominent in wolves *(Canis lupus)*. The maturing female often leaves her natal pack with the unrelated male and forms a territory at the edge of her natal pack's territory [2]. The maturing females remain in the pack as long there is sufficient food for all members of the pack. When food becomes scarce and the competition over food becomes severe among the members of the pack, the maturing males and females leave their natal pack and search for food in other areas [1].
Mitochondrial DNA analysis have shown that the dogs (*Canis lupus familiaris*) have descended from the Asiatic wolves (*Canis lupus chanco*) [3]. During the process of domestication the dogs have undergone both behavioural and physiological changes. The dogs have shifted from a monestrous to diestrous cycle. The feral dog, dingo (*Canis lupus dingo*) in Australia survive by hunting large prey animals. Due to the seasonal availability of prey animals in Australia, the dingoes have retained the monstrous cycle of the wolves. Alloparental care is also observed in dingoes. An offspring of the previous litter usually helps their parents raise the newest litter of pups [4].
Indian free-ranging dogs are diestrous but each female usually produces only one litter per year [5]. Indian free-ranging dogs lack the reproductive hierarchy of the wolf packs and their mating system is promiscuous. In this system many females often give birth near each other at around the same time of year [6]. The Indian free-ranging dogs have adapted to a scavenging lifestyle [7]. Although the dogs live in small groups or singly [8], due to the scarcity of food in their urban environment dogs normally scavenge singly. Dog aggregations can be seen at feeding sites (dumps, dustbins) where hostile interactions take place between the different dogs [9] and sometimes dog groups have been observed to hunt large prey in rural environments [10].
Maternal care is the primary care received by pups in pet's dogs [11] and free-ranging dogs. Suckling and huddling are the main types of care the mother provided during the early weeks

of the puppies lives. As the pups get older food provision by regurgitation [12] and guarding becomes the primary forms of maternal care. Paternal care has not been observed in pet dogs. Paternal care has been reported in Indian free-ranging dogs. Paternal care is mainly provided by guarding the pups during the mother's absence [13]. Alloparental care in free-ranging dogs has been reported to be absent in some countries like Italy [14] and Mexico [15]. Alloparental care in dogs has also been reported to be recently found in Indian free-ranging dogs [16] and in pet dogs [17]. In case of pet dogs play behaviour is the only alloparental care that has been reported. Alloparental care in pet dogs was observed only in the case of intact young females [17]. Males did not show any alloparental care [17]. In case of Indian free-ranging dogs alloparental care has been recorded in related females (grandmother) [16] and males (exact genetic relationship between the pups and the male alloparent was not known) [18].

In the case of pet dogs, the reproduction of the dogs are completely controlled by humans. The pups are usually sold or adopted out as soon as they are weaned. This situation prevents the dog family unit from remaining in close contact with each other [17]. The companions for the dogs are also decided by humans. The companion dogs are usually unrelated to each other. The lack of dog family members in the same area and difficulty in obtaining permission to study pet dogs in another person's house make it difficult to study alloparental care among close genetic relatives in pet dogs. Free-ranging dogs are dependent mainly on humans for their food supply but they are not under direct human supervision [19]. The dogs are able to choose their own mates and companions. This situation may enable close genetic relatives to remain close to each other. This situation makes free-ranging dogs good model animals to study alloparental care among close relatives in domestic dogs. In this study we recorded the alloparental care that had been provided by an older sibling towards her younger siblings.

Materials and methods

The study was conducted in the area surrounding Peerless Nagar, Sodepur (22.69^0 N, 88.38^0E), Panihati municipality, North 24 Parganas district, West Bengal, India. The focal individuals for this study were an young female free-ranging dog (designated as RF), an old male free-ranging dog (designated as MM) and the surviving offspring of RF's first litter (designated as L1F). The housing complex of Peerless Nagar consists of three dog groups which occupy three distinct area (as was observed during the course of the study). The males of all three dog groups were neutered 4 years before the beginning of this experiment to control the dog population in the housing complex but the females were left intact due to the higher cost and longer post-operative care associated with spaying of females (data obtained from questionnaire survey of Peerless Nagar Management Community). All three dog groups were fed by people in peerless Nagar (the two dog groups in the interior by the residents and the dog group at the gate by the security guards). The dogs were mainly fed rice with dal once a day and sometimes biscuits were also given to them by some of the residents (data obtained from direct observations and questionnaire survey of residents of the housing complex). No litter of puppies had been born at Peerless Nagar for nearly four years. New males were prevented from entering the housing complex by the neutered males present in the area. Each dog group in Peerless Nagar guarded their own territory and attacked any dog from the other two groups which tried to approach their territory preventing the intact females of the interior dog groups from leaving and mating with intact males present outside Peerless Nagar (data obtained from direct observations and questionnaire survey of the residents). The members of the dog group at the gate (designated at gate dg) roamed from the gate to a chicken meat shop about 20 metres outside the gate. After the chicken meat shop there was a Bharat Petroleum petrol pump and on the other side of the Petrol pump was another chicken meat shop. The petrol pump and the second chicken meat shop was the territory of a different group of dogs. This dog group (designated as outside dg) consisted of two adult males, three adults females and two pups of about 5months old (the exact relationship between the members of this dog group except for the mother and pups could not be determined). The members of the outside dg chased away any member of the gate dg that tried to approach them preventing the female members of gate dg from mating with any intact outside males (data obtained from direct observations). RF was one of the dogs of the last litter that was born in Peerless Nagar.



1. Gate dog group core territory (2M, 2F)
2. Peerless Nagar
3. Meat shop at the outskirts of gate dog group territory
4. Petrol pump
5. Outside dog group territory (2M, 3F, 2 pups)

Fig 1: Pictorial representation of the location of the territories of Gate dg (2M, 2F) and Outside dg (2M, 3F, 2Pups) (Name of each coloured area has been denoted in the same colour).

The members of the gate dg at the time of the study consisted of only four members -RF (nearly 5 years old), another adult female (nearly 10 years old), a male (nearly 5 years old-injured with a broken leg, he was kept at the flat of a resident) and an older male which was critically ill and died during the course of the study. MM was not from the gate dg. He wandered into the gate dg territory from the outside. The exact origin of MM was not known. MM was also not a member of the outside dg. The experimenter could not determine any information about MM's past. The lack of any healthy male members of the gate dg enabled MM to slowly enter gate dg's territory. Mating between RF and MM was observed. No mating interactions between MM and the other female gate dg member was observed. The other female generally avoided any interactions with MM. RF used the area below the stairs to UCO bank in the Peerless Shopping Plaza as the den site for her first litter. RF was observed to give birth to 10 puppies in the 2nd week of December 2016. 4 of the puppies died within 2 days after birth (data obtained from security guards). The remaining six puppies lived to be 4 weeks old where 3 were adopted by the residents. The experimenter could not get the permission from the adopting residents to observe the growth of these three puppies. The remaining three lived to be 3 months old where two were killed in road accidents. Remaining one puppy survived till adulthood. The surviving puppy was a female (designated as L1F).

L1F stayed with MM and RF in the gate dg territory. Mating between MM and RF was again observed in early October 2017. RF was observed to give birth in the last week of December 2017. RF used the backside of bps Xerox centre in the Peerless Shopping Plaza as her den site. The first weeks of the pups' lives could not be observed. The pups (3 in number) were first seen at 2 weeks old (gender could not be determined at this stage). One puppy was run over by a car at approximately 3 weeks old. The remaining two puppies (both male) survived till 6 months old. The experimenter conducted behavioural observations on the interactions among RF, RF's second litter, MM and L1F. The observations were carried out for 12 weeks (09 January 2018-31 March 2018). We conducted both scan and all occurrence sampling (AOS) in two sessions, each of two hours, morning session (800hrs - 1000hrs) and afternoon sessions (1400hrs-1600hrs). Each session consisted of equal number of AOS and scans. Thus we had 336 hrs of data consisting of 2688 scans and AOS. We calculated average time (hours/week) spend by RF, MM and L1F in guarding the pups from the scan data. We also divided the play interactions between the pups and RF, MM and L1F into -Active play and Passive play. We calculated rate (frequency/ week) at which play was initiated between the pups and any one of the adult dogs from the AOS data. A list of the Active play and Passive play behaviours used in the analysis has been provided in Table 1.

Table 1: Behaviours observed during all occurrence sampling

Active play	Passive play
Play biting/ Play fighting	Lying down while pups play on/ around the adult
Chasing	
Tug of war with cloth, wood etc	
Moving tail and allowing pups to attack it	

We also calculated the relationship between the play initiations (between L1F and the pups) and the increasing age of the pups. We conducted food sharing experiment with the pups and each of the adults individually. In this experiment we placed three pieces of chicken intestine (each 1 cm in length) in a circular paper plate in front of the pups and one of the adults (chicken intestine was used as dogs readily obtained this from the chicken meat shop and it was soft enough that the pre-weaned pups could also eat it). We recorded the number of times the food was shared between the two pups and any one of the adults from the recorded AOS data. In this experiment even if only one pup got to eat or the adult gave all the food to the pups and did not eat at all, it was still considered as a positive food sharing incident and recorded in the data. Finally we calculated the relationship between food sharing incidents (between the pups and any one of the adults) and the increasing age of the pups. All statistical analysis was carried out using statistic XL v 1.8.

Ethical note

The experiments were conducted using non-invasive techniques and without causing harm to the dogs. The food used in this experiment was prepared fresh every day.

Results

We performed Anova test on the average time each of the individuals (RF, MM, L1F) spend guarding the pups per week. We found significant difference in the amount of time each individual spend guarding the pups (Anova test: F=27.723, df=2, p=0.0001). RF was found to spend the maximum time and MM the least amount of time on guarding the pups. L1F spend moderate amount of time guarding the pups (refer to figure 2)

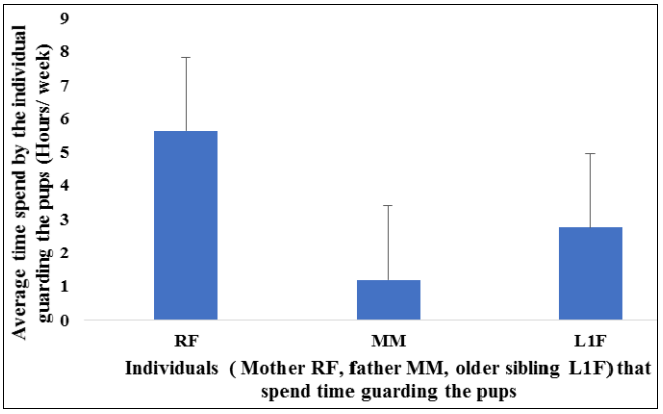


Fig 2: Average time spend by each individual (RF, MM and L1F) on guarding the pups. RF spend the maximum, L1F spend moderate and MM spend the minimum time guarding the pups (Anova test: F=27.723, df=2, p=0.0001)

We performed Kruskal-Wallis Test on the frequencies of passive play behaviours between the pups and each one of the individuals (RFMM, L1F). No significant difference was found (Kruskal-Wallis Test: H=15.3026, critical chi-square value at $p<0.05$ =16). No instances of active play behaviour was observed between the pups and MM (refer to figure 3). We performed Mann-Whitney test on the frequencies of active play behaviours between the pups and each one of the two individuals (RF and L1F). The difference was significant (Mann-Whitney test: U=1, df=12, p=0.00058). We performed Wilcoxon Paired Sample test on the frequencies of passive and active play behaviours between the pups and either one of the two individuals (RF and L1F). In case of RF, we found that passive play behaviours were performed at a higher frequency (T=60.5, df=12, p=0.002). In case of L1F, we found that active play behaviours were performed at a higher frequency (T=18, df=12, p=0.000076).

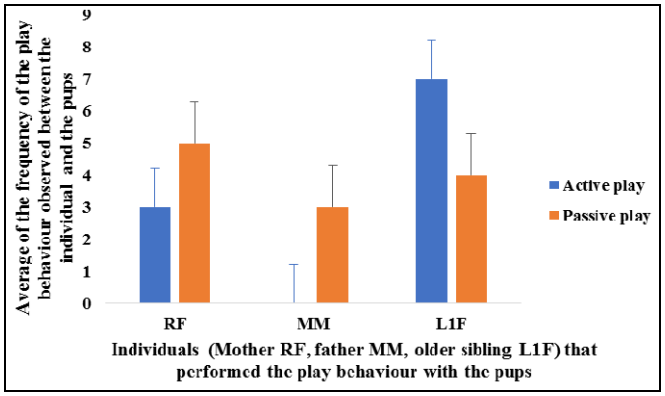


Fig 3: Average of the frequencies of passive play and active play behaviours between the pups and each of the individuals (RF, MM and L1F)

We performed Spearman's rank correlation coefficient test on the average of the frequencies of play initiations (between the pups and L1F) and the increasing age of the pups. We found that there was a positive correlation between the play initiations (between L1F and the pups) and the increasing age of the pups [R_s= (+) 0.9788, p=0.001] (refer to figure 4).

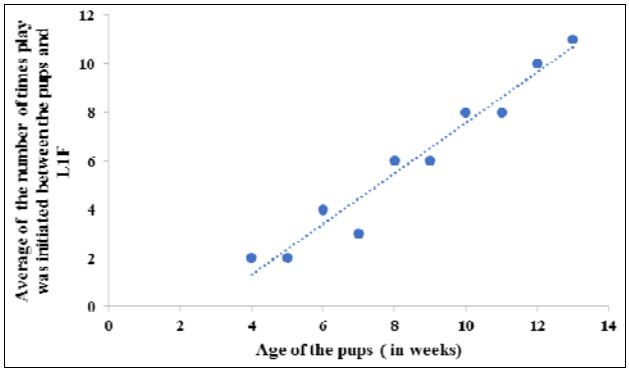


Fig 4: Correlation between the average of the frequencies of play initiations (between the pups and L1F) and the increasing age of the pups. The correlation is significant [Spearman's rank correlation coefficient test: R_s= (+) 0. 9788, p=0.001]'

We performed linear regression test between the average of the frequency of food sharing incidents between the pups and RF. There was a significant decrease in food sharing incidents between the pups and RF with increasing age of the pups (Linear regression test: R^2=0.7811, p=0.00157) (refer to figure 5)

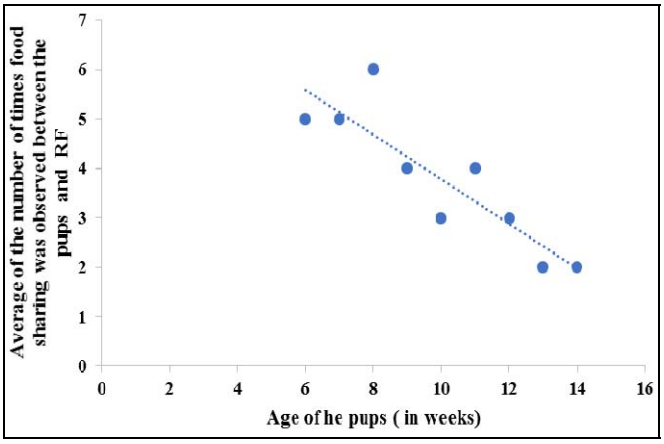


Fig 5: Decrease in the frequency of food sharing incidents between RF and the pups with increasing age of the pups (Linear regression test: R^2=0.7811, p=0.00157)

We performed linear regression test on the average of the frequency of food sharing incidents between L1F and the pups. There was a significant decrease in food sharing incidents with increasing age of the pups (Linear regression test: R^2=0.504, p=0.03) (refer to figure 6)

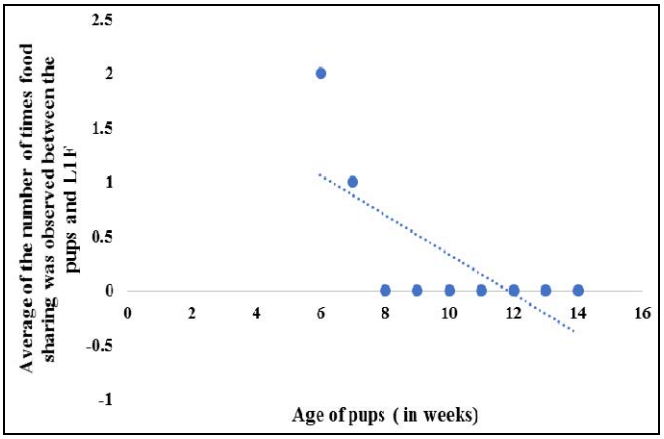


Fig 6: Decrease in the frequency of food sharing incidents between L1F and the pups with increasing age of the pups (Linear regression test: R^2=0.504, p=0.03)

No food sharing incidents was observed between MM and the pups.

Discussion

The production of offsprings is not the only way that animals can pass their genes into the future generations. Inclusive fitness can be gained both by direct offspring production and by indirect rearing of close genetic relatives. Offspring shares 50% of the parent's genes. Full siblings share 50% of the animal's genes whereas half- siblings share 25% of the animal's genes. So same amount of inclusive fitness is gained by caring for one full-sibling or two half-siblings as is gained by rearing one offspring. An animal can increase the representation of its own genes in the future generations by not only producing offsprings but also by helping to rear its genetic relatives [20, 21, 22]. This behaviour can be seen in many group living animals like wolves [1], meerkats [23] etc. The groups usually consist of a mated pair, their offsprings and sometimes siblings of the mated pair [1, 23]. The offsprings of the past litters usually help their parents to rear the youngest generation of offsprings [1, 23]. The past litters' offsprings gain inclusive fitness indirectly through their younger siblings.

Dogs have altricial offsprings. In altricial animals, the offsprings are born blind, deaf and have limited mobility. The puppies need the mother's help in maintaining normal body temperatures, elimination of bodily wastes (defecation and urination), food supply (suckling) and protection from other animals. The puppies' social and physical development defends mainly on interactions with the mother [11]. Studies on the maternal behaviour of Indian free-ranging dogs show that the mother spends most of her time huddling together with the pups in the den during the early weeks of the pups' lives. The mother only ventures away from the pups to forage during the first weeks of the pups' lives [24]. This study shows that the mother (RF) spends the maximum time guarding the pups. Behavioural studies on mother dogs show that the mother spends 65% of her time with the pups during the first month of the pups' lives [16]. In most species of canids some form of male parental care is observed. The most common form of care provided by males in group living canids like African wild dogs [7] (*Lycaon pictus*), wolves [1] (*Canis lupus*) was active defence of the young, care to the mother (by food provisions) and providing food to the young (by regurgitation). The study shows that male MM spend the least amount of time guarding the pups. Studies on the parental behaviour of Indian free-ranging dogs have shown that the fathers guard the pups only during the early weeks of the pups' lives when the mother is absent [13].

In many species of canids older offsprings help their parents raise the newer generation of pups. In black- backed jackals (*Canis mesomelas*) some of the older offsprings help their parents raise subsequent litters of pups by provisioning food and guarding the younger offsprings. Studies have shown that jackal families with helper older offsprings have a higher pup survivorship that jackal families without helpers [26]. In this case the jackals are increasing their genes' representation in future generations indirectly through sibling rearing before they start reproducing their own offsprings. Studies on domestic dogs have shown that young intact females around 1 year old show the strongest reaction to the whining of puppies [17]. In the case of this study L1F has the same mother (RF) as the new litter of pups. Although in both cases (L1F litter and the two pups litter) RF was observed to mate with MM, without DNA analysis the experimenter could not be completely certain that MM was the father in both cases. Observations were done only at fixed time intervals so there was a slight chance that while the experimenter was away RF had mated with another male. So L1F was confirmed to share at least 25% of her genes with the second litter pups (RF was the mother in both case). In case L1F and the two pups were half -siblings, L1F gained the same amount inclusive fitness from the survival of the two pups as she would have from the survival of one of her own offspring. In case MM was the father in both cases then L1F would have gained the same amount of inclusive fitness from two pups' survival as she would have from the survival of two of her own offsprings. In either cases L1F would have benefited from the two pups' survival. The experiment showed that L1F spend moderate amount of time guarding the pups. Studies on the alloparental behaviour of Indian free-ranging dogs have shown that related females spent significant time guarding pups that are not their own [16,18].

In the order carnivora, play behaviour consists of motor patterns that are characteristics of agonistic, courtship and predatory behaviours. Studies on domestic dogs have shown that play is performed routinely, even in adult dogs, both with inanimate objects and socially with their human owners and other dogs [27]. Dogs have shown to handicap themselves when playing with weaker partners to keep the game going rather than winning easily [28]. The study has shown that all three dogs engaged in passive play with the pups but active play between the pups and only two adults (RF and L1F) was observed. Although studies on free-ranging dogs have shown play behaviour of adult males with young pups existed [18], it was not observed in this study. Studies done on maternal care of pups in Indian free-ranging dogs have shown that the mothers replaced pile sleeping and suckling behaviours with guarding and play behaviours as the pups got older [18]. In this study L1F was found to engage in more active play behaviours than RF. L1F was observed to increase play initiations with the pups as the pups got older. Studies on domestic dogs have shown that other than the mother, young (about 1 year old) intact females showed the strongest interest to whining pups. These young females were more likely to interact with the pups in a friendly manner and play with the pups than older dogs [17]. In Indian free-ranging dogs 69% of the care provided by the fathers or any alloparent consists of guarding and play. The pups receive more care (in the form of play and guarding) from the alloparent as they get older and venture away from the security of the den site [18].

The free-ranging dogs begin eating solid foods around 1 month old. The mother regurgitates food to feed them. She sometimes also hunts small prey animals to feed them [13, 24]. In this experiment it was observed that food sharing between RF and the pups decreased with increasing age of the pups. In Indian free-ranging dogs the mothers begins to compete over food with the pups during weaning stage of the pups' lives as the mother starts to prepare for the next breeding season. The competition over food between the mother and the pups increases with increasing age of the pups [29]. Although no food sharing behaviour was observed between the father MM and the pups, dog fathers have been observed in other studies to regurgitate food to feed their pups [13]. In this study L1F was observed to share her food with the pups only for a short time. In free-ranging dogs suckling pups by females other than their mother has been observed [18].

Indian free-ranging live mainly by scavenging from dumping sites and begging humans for food. They have become adapted to a scavenging lifestyle [7]. As the food resources are limited and there is fierce competition at the feeding sites so the dogs mainly live singly instead of in large packs like wolves. One of the factors determining wolf pack size is the availability of prey. Wolves are found in large packs in areas which have large sized preys as the greater numbers enable the smaller sized wolves to take down the larger sized preys [1].In areas where food resources are scarce smaller size wolf packs are found. In Italy wolf packs consist of only the mated pair in the winter due to the scarcity of food. The wolf packs in Israel are also small as the wolves live mainly on small animals and garbage [1].

In the area of the study the dog groups were able to form because there was a constant supply of food. This allowed the older offsprings to remain in the same area as their parents without facing too much competition over food. Increase in the number of dogs also enables the dogs to be better able to protect their area from other dogs and ensure they keep the food supply only to themselves. This situation also enables close relatives to remain in the same area and help protect new pups. Indian free-ranging dogs face high mortality especially during the early weeks of the dogs' lives. In such an environment any additional care provided to the dogs during the vulnerable puppy stage may significantly increase their chances of living to adulthood.

Conclusion

The presence of constant food supply enabled the older sibling to remain in the same area as her parents. This enabled the older sibling to come in contact with the younger siblings. The older sibling provided care to the younger ones mainly through guarding, play interaction and food sharing during the very early weeks of the younger ones' lives. The father also provided care mainly through guarding the pups. The extra care provided by the father and the older sibling may help to increase the chances of the younger siblings surviving long enough to reach adulthood.

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References

1. Mech LD, Boitanni L. Wolves: Behaviour, ecology and Conservation. 1st edition, University of Chicago Press, Chicago, 2003, 1-37.
2. Mech LD, Nelson ME. Non-family wolf (*Canis lupus*)

packs. Canadian Field-Naturalist. 1990; 104:482-483.
3. Savolainen P, Zhang Y, Luo J, Lunderberg J, Leitner T. Genetic Evidence for an East Asian Origin of Domestic Dogs. Science. 2002; 298:1610-1613.
4. Thomson PC. The behavioural ecology of dingoes in north-western Australia. I. Activity patterns, breeding season and pup rearing. European Journal of Wildlife Research.1992; 19:519-529.
5. Pal SK. Reproductive behaviour of free-ranging rural dogs in West Bengal, India. Acta Theriol. 2003; 48:271-281.
6. Pal SK. Mating Systems of Free-ranging Dogs *(Canis familiaris)*. International Journal of Zoology. 2011; 2011:1-10.
7. Bhadra A, Bhadra A. Preference for meat is not innate in dogs. Journal of Ethology. 2014; 32:15-22.
8. Sen Majumdar S, Bhadra A, Ghosh A, Mitra S, Bhattacharjee D, Chatterjee J *et al*. To be social or not to be social: foraging associations of free-ranging dogs in an urban ecosystem. acta ethologica. 2014; 17:1-8.
9. Pal SK, Ghosh B, Roy S. Agonistic behaviour of free-ranging dogs *Canis familiaris* in relation to season, sex and age. Applied Animal Behaviour Science 1998; 59:331-348.
10. Vanak AT, Gompper ME. Dietary niche separation between sympatric free-ranging dogs and Indian foxes in Central India. Journal of Mammalogy. 2009; 90:1058-1065.
11. Lezama KG, Mariti C, Mota DR, Burnes JM, Garcia HB, Gazzano A. Maternal behaviour in domestic dogs. International Journal of Veterinary Science and Medicine. 2019; 7:20-30.
12. Malm K. Regurgitation in relation to weaning in domestic dogs: A questionnaire study. Applied Animal Behaviour Science. 1995; 43:111-122.
13. Pal SK. Parental care in free-ranging dogs, *Canis familiaris*. Applied Animal Behaviour Science. 2005; 90:31-47.
14. Matter HC, Daniels TJ. Dogs, Zoonoses and Public Health. 1st edition, CAB International, Wallingford, 2000, 17-62
15. Coppinger R, Coppinger L. A New Understanding of Canine Origin, Behaviour and Evolution. 1st edition, University of Chicago Press, Chicago, 2002, 45-68.
16. Paul M, Sen Majumdar S, Bhadra A. Grandmotherly care: A case study in Indian free-ranging dogs. Journal of Ethology. 2014; 32:75-82.
17. Pongracz P, Sztruhala SS. Forgotten But Not Lost-Alloparental Behaviour and Pup-Adult Interactions. In Companion Dogs. Animals (Basel). 2019; 9(12):1011-1019.
18. Paul M, Bhadra A. Do dogs live in joint families? Understanding alloparental care in free-ranging dogs. http://www. Researachgate.net/publication/304858083. 01 July, 2016
19. Serpell J. The domestic dog: its evolution, behaviour and interactions with people. 2nd edition, Cambridge University Press, Cambridge, 2017, 342-368.
20. Hamilton, W.D. The genetic evolution of social behaviour. I and II. Journal of Theoretical Biology. 1964; 7:1-52.
21. Manning A, Dawkins MS. An introduction to animal behaviour. 6th edition, Cambridge University Press, Cambridge, 2015, 316-324.
22. Gadagkar R. Survival Strategies: Cooperation and Conflict in Animal Societies. 1st edition, University Press, Hyderabad, 2015, 68-76.
23. Russell AF, Youing AJ, Spong G, Jordan NR, Clutton-Brock TH. Helpers increase the reproductive potential of offspring in cooperative meerkats. Proceedings of the Royal Society B. 2007; 274:513-520.
24. Pal SK. Maturation and development of social behaviour during early ontogeny in free-ranging dog puppies in West Bengal, India. Applied Animal Behaviour Science. 2008; 111: 95-107.
25. Malcolm JR. Parental Care in Canids. American Zoologist. 1985; 25:853-856.
26. Moehlman PD. Jackal helpers and pup survival. Nature. 1979; 277:382-383.
27. Bradshaw JWS, Pullen AJ, Rooney NJ. Why do adult dogs 'play'? Behavioural Processes. 2015; 110:82-87.
28. Ward C, Bauer EB, Smuts BB. Partner preferences and asymmetries in social play among domestic dogs, *Canis lupus familiaris*, littermates. Animal Behaviour. 2008; 76:1187-1199.
29. Paul M, Sen Majumdar S, Bhadra A. Selfish mothers? An empirical test of parent -offspring conflict over extended parental care. Behavioural Processes. 2014; 103:17-22.