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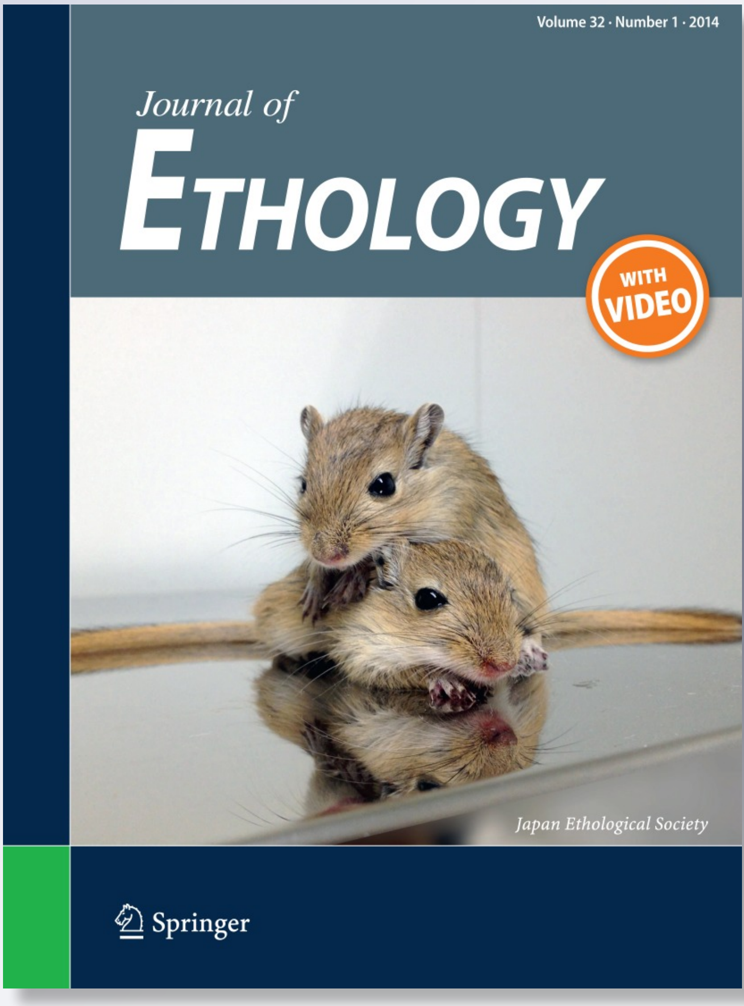

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ARTICLE

Preference for meat is not innate in dogs

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Abstract Indian free-ranging dogs live in a carbohydrate-rich environment as scavengers in and around human settlements. They rarely hunt and consequently do not encounter rich sources of protein. Instead, they have adapted to a diet of primarily carbohydrates. As descendents of the exclusively carnivorous wolves, they are subjected to the evolutionary load of a physiological demand for proteins. To meet their protein needs, they resort to a Rule of Thumb—if it smells like meat, eat it. Pups face high competition from group and non-group members and are in a phase of rapid growth with high protein demands. Following the Rule of Thumb, they can acquire more protein at the cost of increased competition and reduced supplementary non-protein nutrition. However, if the mother supplements their diet with protein-rich regurgitates and/or milk, then the pups can benefit by being generalists. Using a choice test in the field, we show that, while adults have a clear preference for meat, pups have no such preference, and they even eagerly eat degraded protein. Thus, the Rule of Thumb used by adult dogs for efficient scavenging is not innate and needs to be learned. The Rule of Thumb might be acquired by cultural transmission, through exposure to meat in the mother's regurgitate, or while accompanying her on foraging trips.

Keywords Scavengers · Dogs · Rule of Thumb · Innate · Pups · Cultural transmission

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Introduction

Adult food preferences in mammals are shaped by genetic predispositions (Scott 1946; Nachman 1959) and by subsequent learning experiences (LeMagnen 1967; Rozin 1967). For example, the flavor of mother's milk provides cues such that the pups preferentially eat what the mother did, in rats (Galef and Henderson 1972) and also in pigs (Campbell 1976). The swallowing of amniotic fluid before birth seems to affect food preference in the adult stage in humans (Mennella and Beauchamp 1994) and in sheep (Mistretta and Bradley 1983), suggesting that learning can begin even before birth. The peripheral gustatory system of puppies is already developed at birth but does not reach the adult form until later in life (Ferrell 1984a), such that genetic predispositions can constrain taste perception. Early experiences of food also seem to have an impact on dog food preference (Kuo 1967; Mugford 1977; Ferrell 1984b) which is strongly influenced by the mother, through offering regurgitated partly digested food before weaning (Thorne 1995) and also through foraging in the presence of the pup.

Besides the possibility of the strong influence of mother's diet on pups, the pup's own experience also shapes its diet. Evidence of learning has been seen in dogs where flavor experience and physiological effect are well separated in time, such that classical conditioning is inadequate for an explanation (McFarland 1978). Neophobia or fear of something new is uncommon in dogs, but it has been reported in the case of food (Thorne 1995). Neophilia or preference for something new is common when it comes to food (Mugford 1977; Griffin et al. 1984). Aversion develops rapidly for food which have a negative physiological response, as has been demonstrated in coyotes (Ellins et al. 1977) and to a lesser degree in dogs (Rathore 1984). So a pup's food preferences may be innate, conditioned by experience or learned either through cultural transmission from the mother or through active teaching by her.

Wolves hunt for meat and occasionally scavenge (Mech and Boitani 2003; Forbes and Theberge 1992), while their modern-day descendents—pet dogs—are fed by their owners in controlled amounts, often leading to over-feeding (German 2006; Edney and Smith 1986; McGreevy and Thomson 2005). Free-ranging dogs exist in many countries, like Mexico (Ortega-Pacheco et al. 2007; Daniels and Bekoff 1989), Ecuador (Kruuk and Snell 1981), Zambia (Balogh 1993), Zimbabwe (Butler et al. 2004), Italy (Boitani 1983; Bonanni et al. 2010), India (Pal 2001; Vanak and Gompper 2009), Nepal and Japan (Kato and Yamamoto 2003), etc. While they do occasionally hunt and beg for food, they principally acquire food by scavenging (Vanak and Gompper 2009; Vanak et al. 2009; Spotte 2012), making them an ideal model system to study the effects of the earliest form of domestication.

Indian free-ranging dogs have appeared in many ancient Indian texts and folklore over the ages, sometimes as a domesticated animal and sometimes as a stray (Debroy 2008). They have lived in their current state in India for generations and are well adapted to the scavenging lifestyle such that, today, they are an integral part of the human ecology (Pal 2001). Indian free-ranging dogs do not often encounter meat during scavenging in waste dumps and while begging for food. Instead, they live on a carbohydrate-rich omnivorous diet consisting of biscuits, breads, rice, lentil, fish bones, and occasional pieces of decomposing meat from a carcass (and even mangoes, cow dung, and plastic; Bhadra et al., unpublished data). These dogs have adapted to their scavenging habit without actually giving up the preference for meat (Houpt et al. 1978; Bhadra et al., unpublished data). A possible mechanism might have been the development of better digestion of carbohydrates. It is known that dogs are omnivorous animals, adapted to a human-like diet, which might have been the result of their long history of domestication (National Research Council 2006). This is substantiated by more recent genetic analysis showing that the ability to digest carbohydrates was one of the major genetic changes that the ancestors of dogs underwent during their transition from wolves (Axelsson et al. 2013). Given the carbohydrate-rich diet of these dogs, this would be an advantage in terms of meeting their energy requirements, especially in areas like India where the human diet is chiefly comprised of carbohydrates (Mohan et al. 2009). However, it seems that the dogs have behaviorally adapted to scavenging in and around human habitation by developing a Rule of Thumb for foraging—"if it smells like meat, eat it". This would enable them to always choose the food with a higher intensity of meat smell first, thus helping them sequester higher amounts of protein in their diet (Bhadra et al., unpublished data). We wanted to test the hypothesis that this Rule of Thumb is an innate characteristic of the dogs and does not need to be learned.

Materials and methods

We used the one-time multi-option choice test (OTMCT) module for our experiment (Bhadra et al., unpublished data). The experimenter walked on the streets to locate dogs that were solitary, and used these for the trials. If other dogs were present in the vicinity, then the focal dog was lured away to ensure that there would be no disturbance during the trial. Thus, dogs were chosen at random, as and when they were encountered on the streets. The dog was provided with three food options simultaneously such that all three were equally physically accessible. For this, the experimenter placed the three food items about 5 cm (2 in) from each other on a piece of cardboard and presented this to the dog. The three food items were placed in a randomized fashion on the board across trials (see the video in ESM for details). All events including the inspection and eating of the food options were recorded in the order of their occurrence. In the event of any other dog approaching the food or interacting with the focal dog, the trial was aborted. The data for only those cases where all the options were at least inspected were used for analysis. Based on our qualitative observations, inspection was defined as "approaching within 2.5 cm (1 in) of the food with the snout extended and then sharp inhalation with flared nostrils". These dogs, living in a highly competitive environment, could be expected to eat the preferred food first, and so we recorded the order in which the food was consumed. The experiments were conducted in Kolkata (22°34′10.92″N, 88°22′10.92″E), West Bengal, India, between December 2011 and March 2012.

In the OTMCT experiments, the quantity of food was too small (<10 ml) to be a stimulus—we used small lumps of food, approximately the size of an almond. The options were provided such that they were visually identical and the only cue for the dogs to make the choice was the odor of each option. Each dog was given the choice test only once to eliminate the effect of learning and to get a clear representation of the preference already formed at the population level. To ensure that we did not resample individuals, we carried out the trials at different localities on different days, and, within a locality for consecutive trials, we used visual identification of dogs and landmarks to eliminate such repeats. The experiment was conducted in two sets, one with adult dogs and the other with pups aged 8–10 weeks. This age window was chosen because the pups learn to take solid food from external sources, begin exploring by themselves and wean at this age (Pal 2008). In each set, our final sample size was 60. Of the adults, 35 were female and 25 were male, while there were 29 females, 23 males, and 8 individuals of unknown sex among the pups sampled.

In the experimental set (Experiment 1A), the pups were given a gradient of proteins in novel food. The options provided in OTMCT were P1 (dog biscuit, 80 % protein); P2 (fresh Pedigree®, 24 % protein); P3 (1-day-old Pedigree®, protein degraded) (please see ESM for detailed composition). In the control set (Experiment 1B), adults were given the same choice test. The dog biscuit actually contained some meat while Pedigree® did not contain animal tissue protein. The dogs often have to search for food amidst rotting garbage, so it is important for them to distinguish between fresh and degraded protein. We used the stale Pedigree® as a source of degraded protein. Neither the pups nor the adults are likely to have been exposed to Pedigree® or dog biscuit. The adults are known to discern between food options by smell (Houpt et al. 1978) and should thus treat the options differently. Since adults follow the Rule of Thumb, they should prefer the dog biscuit with the meat smell and avoid the stale protein. So, for adults, we expected the order of preference to be P1 > P2 > P3. We hypothesized that the juveniles should follow the same order of preference as the adults if the Rule of Thumb is innate.

Absolute choice was defined as the total number of times each option was chosen in a particular experiment. Choice was taken as the complete consumption of a particular option. Eating order was computed for each experiment. A 3 × 3 matrix was constructed with the three options in the columns and the number of times each option was chosen first, second, and third, respectively, in the rows. Now, a contingency Chi-squared test was carried out to determine whether the tables were random. If they were significantly different from random, then the option that was chosen first the highest number of times was taken to be the first preference at the population level. Similarly, the options chosen second and third were also determined.

We computed the average ranks for each event in an experiment, thus getting an idea of the order of occurrence of the inspection and eating of each type of food. Each event was assigned a rank based on the order of occurrence. Since there must be 3 inspections in each experiment and 3 possible acts of consumption, each event could receive a rank between 1 and 6. When an event did not occur (one of the options was not consumed), it was assigned the rank of 7, meaning it had a higher rank than if it had been eaten last. The average of all the ranks for each event was calculated.

Results

From absolute choice, the adults clearly prefer P1 over P2 and P2 over P3 (two-tailed Fisher's exact test; P1−P2: $p < 0.0001$; P2−P3: $p = 0.048$; and P1−P3: $p < 0.0001$) (Fig. 1) whereas the pups prefer all three equally (two-tailed Fisher's exact test; P1−P2: $p = 0.679$; P2−P3: $p = 0.999$; and P1−P3: $p = 0.999$) (Fig. 1). In terms of eating order, adults eat P1 first, P2 second; and P3 third ($\chi^2 = 74.233$, $df = 4$, $p < 0.0001$) (Fig. 2; Table 1), while pups eat the food in random order ($\chi^2 = 3.797$, $df = 4$, $p = 0.434$) (Fig. 2; Table 1). So pups do not discriminate between different foods (i.e., they show neither preference nor aversion) while adults do prefer the meat smell and avoid the food containing degraded protein. The overall rejection rate in adults (96/180) is significantly higher than that in pups (7/180) (two-tailed Fisher's exact test: $p < 0.0001$). Hence, we reject our null hypothesis, and conclude that the Rule of Thumb is not innate.

This result was corroborated by the average ranks of the eating events, where adults clearly showed a hierarchical order of ranks ($\text{Rank}^{P1E} = 4.20 \pm 1.60$, $\text{Rank}^{P2E} = 5.85 \pm 1.64$, $\text{Rank}^{P3E} = 6.73 \pm 0.63$) (Table 2) and pups did not ($\text{Rank}^{P1E} = 4.15 \pm 1.53$, $\text{Rank}^{P2E} = 4.37 \pm 1.78$, $\text{Rank}^{P3E} = 4.20 \pm 1.75$) (Table 2). All inspections occurred in random order (Experiment 1A: $\text{Rank}^{P1I} = 2.93 \pm 1.49$; $\text{Rank}^{P2I} = 2.85 \pm 1.69$; $\text{Rank}^{P3I} = 2.77 \pm 1.58$; Experiment 1B: $\text{Rank}^{P1I} = 2.13 \pm 0.98$; $\text{Rank}^{P2I} = 2.27 \pm 1.01$; $\text{Rank}^{P3I} = 2.35 \pm 1.36$) (Table 2), but eating only occurred after all the choices had been inspected by the adults (mean of ranks of all inspection for adults is 2.25 ± 1.13 and mean of rank of all eatings for adults is 5.59 ± 1.73; two-tailed Mann–Whitney test: $U = 29968.000$, $df1 = 180$, $df2 = 180$, $p < 0.0001$). Interestingly, in the case of the pups, eating did not begin after all three options had been inspected. The pups seemed to inspect a food item and consume it immediately, before inspecting the next available option. The difference in the average ranks for each pair of inspection and eating was nearly equal to 1 (P1 1.22 ± 0.74, P2 1.52 ± 1.33, P3 1.43 ± 1.05) in case of the pups, while it was more variable (P1 2.07 ± 1.47, P2 3.58 ± 1.79, P3 4.38 ± 1.58) in the case of the adults. So, we checked how often inspection of a particular food is followed immediately by its consumption, representing a situation when the pups would be driven by their high hunger levels to eat what is edible immediately, without exploring all available options. We called this possible strategy sniff and snatch (SNS)—this

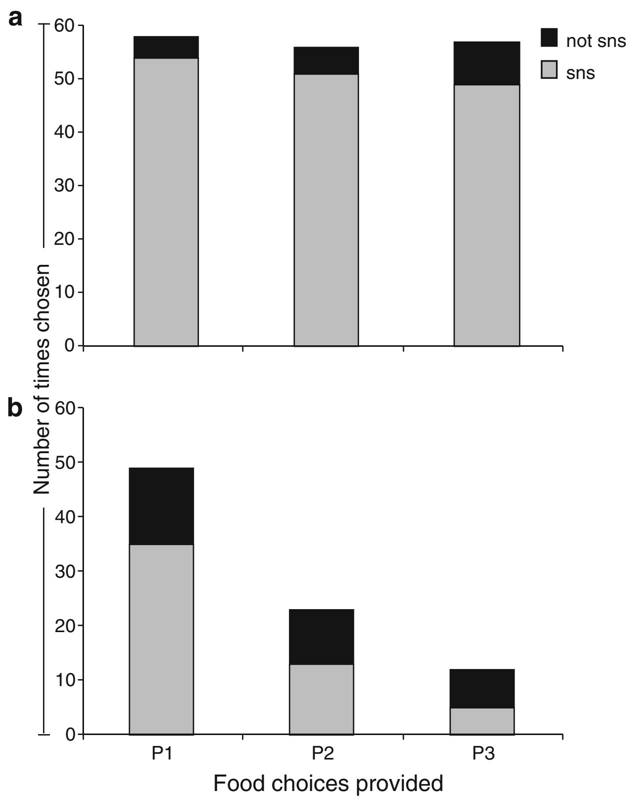

Fig. 1 Absolute choice data and proportion of sniff and scratch (*SNS*) from Experiments 1A and 1B. **a** Absolute choice in Experiment 1A (pups): *P1* (58) = *P2* (56) = *P3* (57) (two-tailed Fisher's exact test; *P1*−*P2*: $p = 0.679$; *P2*−*P3*: $p = 0.999$; and *P1*−*P3*: $p = 0.999$). **b** Absolute choice in Experiment 1B (adults): *P1* (49) > *P2* (23) > P3 (12) (two-tailed Fisher's exact test; *P1*−*P2*: $p < 0.0001$; *P2*−*P3*: $p = 0.048$; and *P1*−*P3*: $p < 0.0001$). Proportion of *SNS* in Experiment 1A (154/173) is significantly higher than that in Experiment 1B (53/84) (two-tailed Fisher's exact test: $p < 0.0001$)

included the cases where the difference between the ranks for eating and inspection of a particular option was 1. 89 % of all choices made by pups were a result of this SNS strategy, which was significantly higher than the 63 % of the adults (two-tailed Fisher's exact test: $p < 0.0001$) (Fig. 1).

Discussion

Adult free-ranging dogs use the Rule of Thumb—"if it smells like meat, eat it"—for efficient intake of proteins through scavenging. This Rule of Thumb could be an innate characteristic of dogs, stabilized through a long history of domestication from wilder ancestors. It is also possible that dogs are not born with the ability to pick out richer sources of protein by smelling meat, but that they learn this over time through a process of cultural transmission or by operant conditioning. Our results clearly show that pups (in the weaning stage) do not follow the Rule of Thumb to make a choice of food. On the contrary, they seem to often inspect a particular food followed immediately by its consumption, a strategy which we call SNS. Thus we conclude that the Rule of Thumb used by adult dogs is not innate, and needs to be acquired at some stage in life.

Our results do not necessarily suggest that the pups are physiologically incapable of distinguishing between food types by smell. The lack of the ability to apply the Rule of Thumb for selection of protein-rich animal tissue may be due to the high dietary requirement of energy and, to a lesser extent, dietary proteins of the growing puppy. The pups are in a phase of rapid growth, have high dietary energy and protein needs, and may not be able to afford to discriminate between foods simply to maintain homeostasis and to deposit tissue. Mother's milk is a highly digestible and rich supply of essential amino acids, fats, and carbohydrates, which ensures efficient sequestering for babies for rapid growth and development (Fox and McSweeney 2003). Pups are fed such milk rich in macronutrients by the mother (of the 22.7 % dry matter in milk, 9.47 % is fat, 7.53 % is protein, and 3.81 % is sugar) (Oftedal 1984). So, for the pups, ther protein:fat:carbohydrate ratio works out to be roughly 36:45:19 % compared to the macronutrient content of 30:63:7 % measured in the diet consumed by adults provided with ad libitum food (Hewson-Hughes et al. 2013). The protein level in milk seems to exceed that required in adults, whereas fats (a rich source of energy) seem to be in deficit, though there is considerable amount of fat in both cases.

As the weaning period approaches, the mother reduces feeding and the pups solicit more food. Around 5–6 weeks, the mother begins to regurgitate solid food (Malm and Jensen 1993, 2010) which is also rich in proteins (for a single group, out of 10 observations, 8 contained meat; Manabi Paul, personal observations). This regurgitation from the mother initiates the training for eating solid food. Around 8–10 weeks of age, the pups begin their own explorations and find food for themselves, but their diet is still supplemented by occasional suckling and regurgitation. Hence, they might not need to specifically sequester proteins even if they are capable of doing so, since the overall requirement for nutrition is so high. This is substantiated by the fact that the pups reject food at a much lower rate than the adults (see "Results"), and, under ad libitum feeding conditions, protein intake increased with increased dietary fats (Ontko et al. 1957).

Dogs are adapted to an omnivorous diet similar to humans (National Research Council 2006), and are capable of digesting carbohydrates better than their ancestors (Axelsson et al. 2013). Pups developing on a low-protein diet might be well adapted to survive on fats and

Fig. 2 Frequency distribution of food choice for determination of eating order in the OTMCT. **a** Pups: eating order is $P1 = P2 = P3$ ($\chi^2 = 3.797$, $df = 4$, $p = 0.434$); **b** adults: eating order is $P1 > P2 > P3$ ($\chi^2 = 74.233$, $df = 4$, $p < 0.0001$)

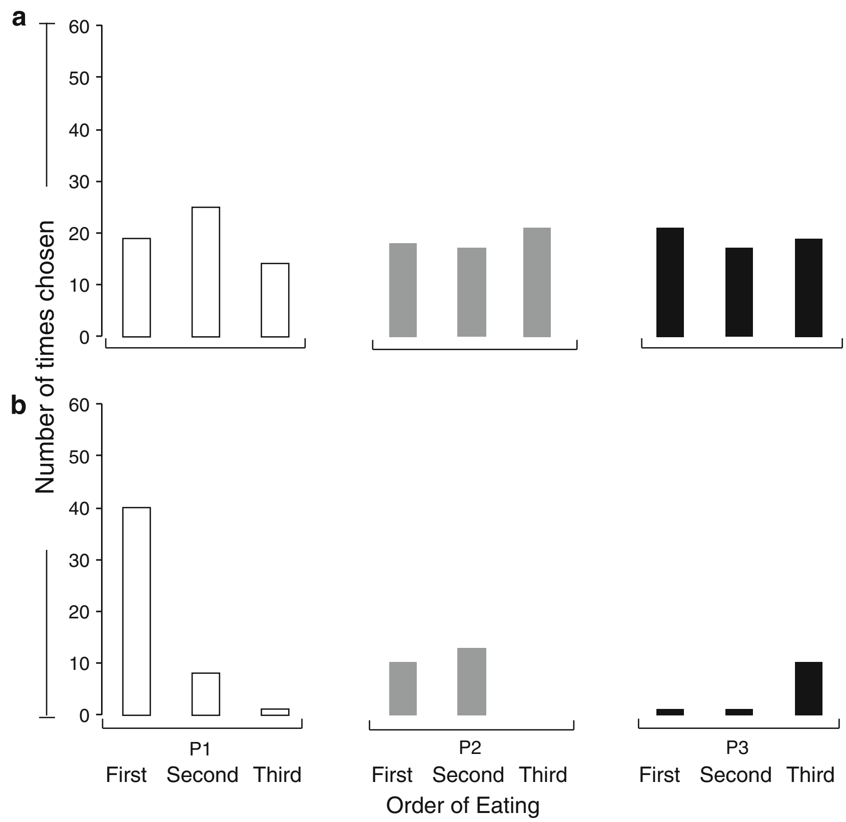

Table 1 The results of the Chi square tests performed to check for preference towards different food types provided in Experiment 1A and 1B

Expt. No.	Chi square value	*p* value for Chi square	Log-likelihood value	*p* value for log-likelihood	*df*	Option chosen first (no. of times)	Option chosen second (no. of times)	Option chosen third (no. of times)
1A (pups)	3.797	0.434	3.786	0.436	4	–	–	–
1B (adults)	74.233	0.000	56.476	0.000	4	P1 (40)	P2 (13)	P3 (10)

Table 2 Average rank (mean ± SD) for each event (inspection and eating of P1, P2, and P3) in Experiment 1A and 1B

Expt. No.	Average rank (mean ± SD)					
	Inspection			Eating		
	P1	P2	P3	P1	P2	P3
1A (pups)	2.93 ± 1.49	2.85 ± 1.69	2.77 ± 1.58	4.15 ± 1.53	4.37 ± 1.78	4.20 ± 1.75
1B (adults)	2.13 ± 0.98	2.27 ± 1.01	2.35 ± 1.36	4.20 ± 1.60	5.85 ± 1.64	6.73 ± 0.63

carbohydrates, though they would need to compensate on their tissue deposition, and hence growth (Waterlow 1986). However, if they supplement the macronutrients received from the mother's milk with any source of energy available to them, they would benefit by being generalists while foraging. Dogs live in stable social groups (Cafazzo et al. 2010) and pups typically tend to forage with adults (Sen Majumder et al. 2013). While foraging, they not only face competition from their siblings but also from adults in the group, including their mother (Paul et al., unpublished data). In such a competitive environment, a generalist feeding strategy can help them to forage efficiently. On the other hand, being generalists makes the pups more vulnerable to feeding on "unsafe" food. Protein degradation creates hydrophobic amino acids that are usually bitter and have a strong odor that is detectable at low concentrations (Mukai et al. 2009). Being scavengers, dogs have a high probability of being exposed to decaying food, and they are likely to avoid food that is toxic or unpalatable. Hence, in our experiment, the stale Pedigree® could be easily detected by the adults and avoided, while the pups, being naïve foragers, did not make any such distinction. Thus, we can surmise that pups would be incapable of toxin avoidance, unlike adults, which can be conditioned to avoid toxins in their diet (Rathore 1984).

Since resources are dispersed over space and time, they are in high demand and require defending (Macdonald 1983; Pal et al. 1998). The pups are not capable of such defense and rely on the mother for it. The mother in turn gathers the food, processes it, and provides it as milk, which is the chief source of energy for the pups. But she cannot continue this for an indefinite amount of time. To prepare her body for the next breeding cycle, she must cut this high cost from her own nutrition budget (Trivers 1974). As a result, she gradually switches to regurgitating food which is less costly and occurs less often than providing milk. Finally, she stops supplementing the pups' nutrition completely. At this point, the pups have already been exposed to solid food in the form of regurgitated material and have begun exploring and foraging by themselves (Pal 2005). Now the Rule of Thumb can take over, being passed on from the mother through a process of cultural transmission (Pryor 2001). In fact, this late development offers some plasticity to the behavior. The pups may get trained to the most concentrated source of protein in the vicinity, as both their mother's regurgitation and their own explorations should expose them to this source. This would then be similar to the observation made in rats (Galef and Henderson 1972) and pigs (Campbell 1976) which develop food preferences based on exposure to certain tastes through their mother's milk. Thus, the development of a preference for meat in dogs can occur by operant conditioning or cultural transmission, or a combination of the two.

Dogs have evolved from carnivorous ancestors to a scavenging, omnivorous lifestyle, possibly coupled with lower protein and fat demands, as they are capable of sequestering energy by utilizing carbohydrates (National Research Council 2006; Axelsson et al. 2013), but it is possible that the adaptation has resulted in reduced growth, leading to the overall reduction of body size of the majority of breeds, which is apparent in dogs as compared to wolves (Morey 1992). Within the lifetime of the individual, a low-protein diet may cause hypoproteinemia in dogs (Weech et al. 1935), and hence they need to maintain an optimal level of proteins in their diet. Predictions of optimal diet theory suggest that partial preferences should develop when fitness is maximized through the rate of food gain maximization, subject to some nutrient being maintained at a minimum threshold value (Pyke 1984), as seen in our experiment. The ability of adult dogs to selectively feed on protein-rich food in a competitive environment would be adaptive, given the nature of resources available to the dogs.

Dogs are subject to the evolutionary load of their ancestors being complete carnivores, and hence they have a high-protein diet (Case et al. 2010) and selectively feed on protein-rich food (Hewson-Hughes et al. 2013). As adults, they acquire proteins by hunting, scavenging, or begging, and have to retain a preference for meat. But as pups, their mother provides the necessary proteins through suckling or regurgitation, and the pups can afford to be generalists in their own foraging bouts. Such a generalist strategy would also serve to minimize competition among siblings over preferred food while foraging as a group, and would benefit the pups by maximizing their calorie intake. Hence, beginning to forage as a generalist and then learning the Rule of Thumb for specifically sequestering more proteins in their diet should be an evolutionarily stable strategy for the dogs. If pups are able to learn the Rule of Thumb without the influence of adults, simply by their own explorations during foraging, operant conditioning would be the more likely mechanism for such learning. However, since pups are typically exposed to regurgitations of the mother and also begin their explorations with her, cultural transmission might play an important role in the learning of the Rule of Thumb, either actively through teaching or passively through social learning. We intend to carry out controlled experiments to test the importance of these two mechanisms in the development of foraging habits of the dogs.

Our results not only show that the Rule of Thumb is not innate but also highlights the importance and influence of early exposure to food for dogs. As their early encounters shape their adult preferences, this emphasizes the role of pet owners in bringing up their dogs. Given that most pups are reared in human homes away from their mothers from a very early age, the diet offered by owners to freshly weaned pups might be crucial in determining the lifetime eating habits of their pets.

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