Strategies in novel food extraction tasks and responses to perceived threats in stray dogs, *Canis familiaris*

A thesis submitted in partial fulfillment of the
requirements for the award of the BS/MS dual degree
at

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Certificate

This is to certify that this thesis entitled 'Strategies in novel food extraction tasks and responses to perceived threats in stray dogs, *Canis familiaris*' represents original research carried out by 'Madhur Mangalam' at 'Indian Institute of Science Education and Research Pune' under the supervision of 'Mewa Singh, Professor, Biopsychology Department, University of Mysore' during the academic year 2011-2012.

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Declaration

I hereby declare that the matter embodied in this thesis entitled ‘Strategies in novel food extraction tasks and responses to perceived threats in stray dogs, *Canis familiaris*’ in partial fulfillment of the requirements for the award of the BS/MS dual degree at ‘Indian Institute of Science Education and Research Pune’ are the results of the investigations carried out by me, under the supervision of ‘Mewa Singh, Professor, Biopsychology Department, University of Mysore’. I also declare that the same has not been submitted elsewhere for the award of any other degree.

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Abstract

Studies on risky foraging strategies have largely ignored the underlying cognitive mechanisms. Behavioral decisions regarding foraging and risk evasion were studied in urban stray dogs by observing their use of alternate strategies in solving novel food extraction tasks under variable risk environments. Use of strategies associated with reduced risk aversion, possibly due to greater nutritional requirements, resulted in higher foraging performance in males and pregnant/lactating females, which behaved similarly. Furthermore, performance was correlated with sensitivity and fearlessness to perceived threats at the level of an individual. These findings demonstrate an intricate interaction between information gathered through sensory mechanisms and the motivational states of animals in influencing decisions pertaining to foraging.

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Introduction

Animals often face the distinct but complementary challenges of identification and optimization returns associated with particular foraging strategies (Sih, 1992; Stephens and Krebs, 1986; Ydenberg, 1998). When food distribution is patchy and foraging time is constrained, returns from conservative foraging strategies are often lower than the caloric requirement of animals (Caraco, 1980; Houston and McNamara, 1982; Real and Caraco, 1986; Sih, 1992; Stephens, 1981; Stephens and Krebs, 1986). Under such conditions, temporary reduction of nutritional intake to match the expected availability provides no long term advantage (Caraco, 1980; Stephens, 1981). It may, therefore, be more advantageous to use risky strategies and that lead to greater returns (Caraco, 1980; Real and Caraco, 1986; Stephens, 1981; Stephens and Krebs, 1986). How foragers tradeoff the enhanced risk and returns can be studied by observing their use of alternate strategies in different situations (Gilliam and Fraser, 1987; Lima and Dill, 1990; Ydenberg, 1998). Since the costs and benefits associated with a behavior depend on life history, physical condition, sex, and age-class of an animal, the variation in use of strategies is likely to exhibit considerable intra-specific differences in foraging performance and risk aversion (Brown and Kotler, 2004; Kacelnik and Bateson, 1996; Stephens and Krebs, 1986). Studies on risky foraging strategies have often observed behavioral adjustments made by animals to optimize the returns under manipulated conditions (Krebs and Kacelnik, 1991; Lima and Dill, 1990; Stephens and Krebs, 1986; Ydenberg, 1998). However, decisions pertaining to foraging are likely to be influenced by the interaction between information gathered through sensory mechanisms and the motivational states of animals, a crucial aspect that has largely been ignored (Shettleworth, 2009; Ydenberg, 1998). Not surprisingly therefore, the relationship between the ecological and cognitive aspects of foraging remains unexplored.

Here, behavioral decisions regarding foraging and risk evasion were studied in urban stray dogs, *Canis familiaris* in Pune, India. These dogs typically forage on garbage, dumped in roadside trash bins. Initially, novel foraging tasks were presented to the dogs, and sex-specific differences in food extraction strategies were observed. Subsequently, to test whether these observations represent motivational differences between males and females, food extraction behavior in pregnant/lactating females, which were hypothesized to behave like males given their greater nutritional requirements, was observed. Finally, to investigate the relationship between performance in the contexts of foraging and the direction of risk evasion in general, dogs were presented with the same task in high threat environment and their extraction behavior was observed.

Methods

Subjects and study locations

Observations were made on 223 individual urban stray dogs, *Canis familiaris* from April 2011 to March 2012 at several locations in Pune (18°28′25″N, 73°47′52″E), India. Most of these locations were alleyways, roadside areas adjacent to garbage bins and unfenced public or private land. It was made sure that each individual was tested only once by scrupulously noting the morphological characteristics of individuals and by carefully selecting only those locations that had that no movement of dogs amongst them. Individuals in poor health or with physical disabilities were not considered for the study.

Food extraction task

The task consisted of food extraction from a specially crafted packet made from corrugated paperboard/plasticboard with a chicken claw inside (Figure 1).

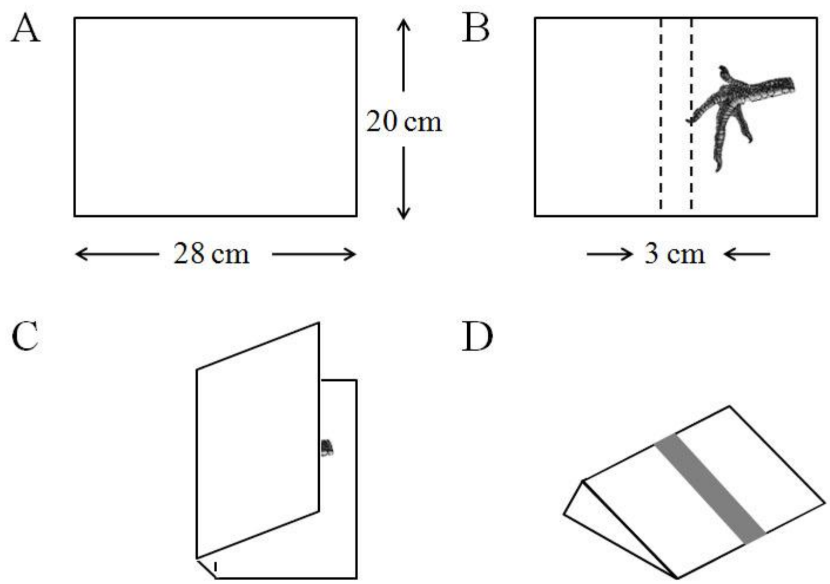


Figure 1. A schematic diagram describing the crafting of food packets used in the experiments. For crafting a packet, a 28cm x 20 cm piece of double-faced corrugated paperboard/plasticboard was folded in a manner such that the resulting structure had two 12.5 cm x 20 cm lateral flaps with a 3 cm backbone running parallel to the corrugated flutes (**A**, **B**). A freshly severed chicken claw was then placed at the middle of the backbone and the flaps were fastened together using 3.8 cm wide polypropylene parcel tape (**C**, **D**).

Experiment 1

Experimental procedure

Paperboard food packets were presented to 105 dogs: 51 males, 54 non-pregnant/non-lactating (NPNL) females and their extraction strategies were observed. All observations were made between 2200 and 0200 hours. A food packet was placed by BG in the vicinity of a dog (2-3m from the subject) that had had no conspecifics within 20 m from it. MM then moved to a spot (blind) from where he was unnoticeable to the subject. Once the packets were placed on the ground, the dogs smelled the food, approached the packets and attempted extraction. An ‘attempt’ was defined when a subject used its mouth to grasp any portion of the packet. The extraction technique and the corresponding latency (interval between the first attempt to open the packet and the ingestion of food) were recorded by MM. The empty packet was then collected by BG and used to double-check the categorization of the extraction technique. Appropriate statistical tests are indicated wherever required.

Results

Males primarily inserted their snout into the packet and pulled out the food with their mouth mostly without damaging the packet – the 'gap-widening technique' (Figure 2A, B; Movie S1). On the other hand, NPNL females generally ripped open the packet with their mouth – the 'rip-opening technique' (Figure 2C, D; Movie S2).

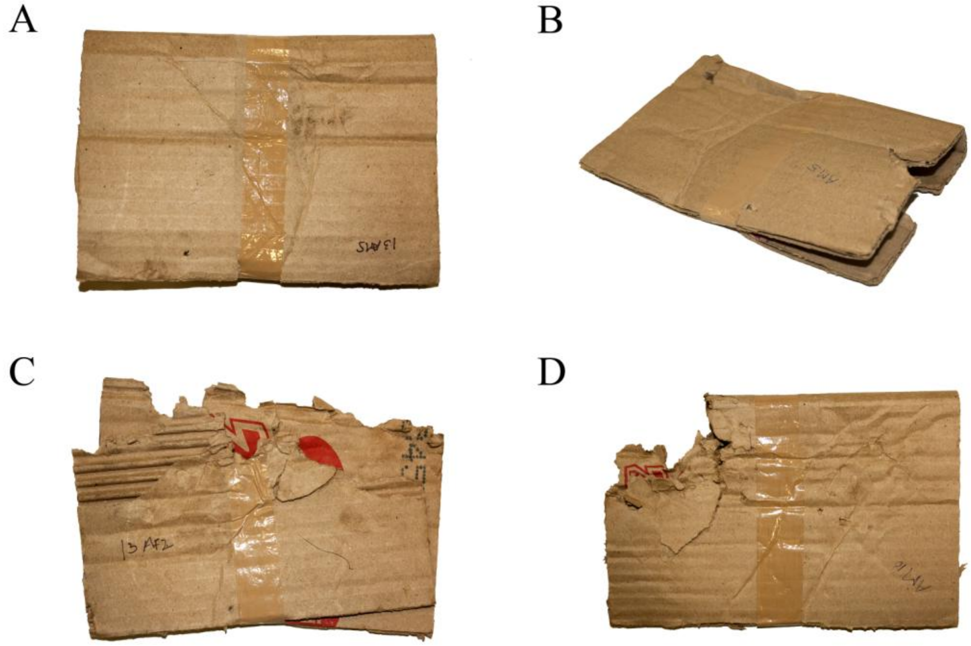


Figure 2. Empty packets recovered from dogs. Packets recovered from dogs that used the gap-widening technique (**A**, **B**) and the rip-opening technique for food extraction (**C**, **D**).

Males used the gap-widening technique frequently (Figure 3A; multi-group proportions test: $\chi^2 = 78.862$, $P < 0.001$), which resulted in faster food extraction (Figure 3B; independent samples t-test: $t_2 = -12.124$, $P < 0.001$). NPNL females 'guarded' food by retreating to a secluded place before attempting extraction (Figure 3C; multi-group proportions test: $\chi^2 = 64.094$, $P < 0.001$), during which they kept the packets covered with their forepaws (Movie S2).

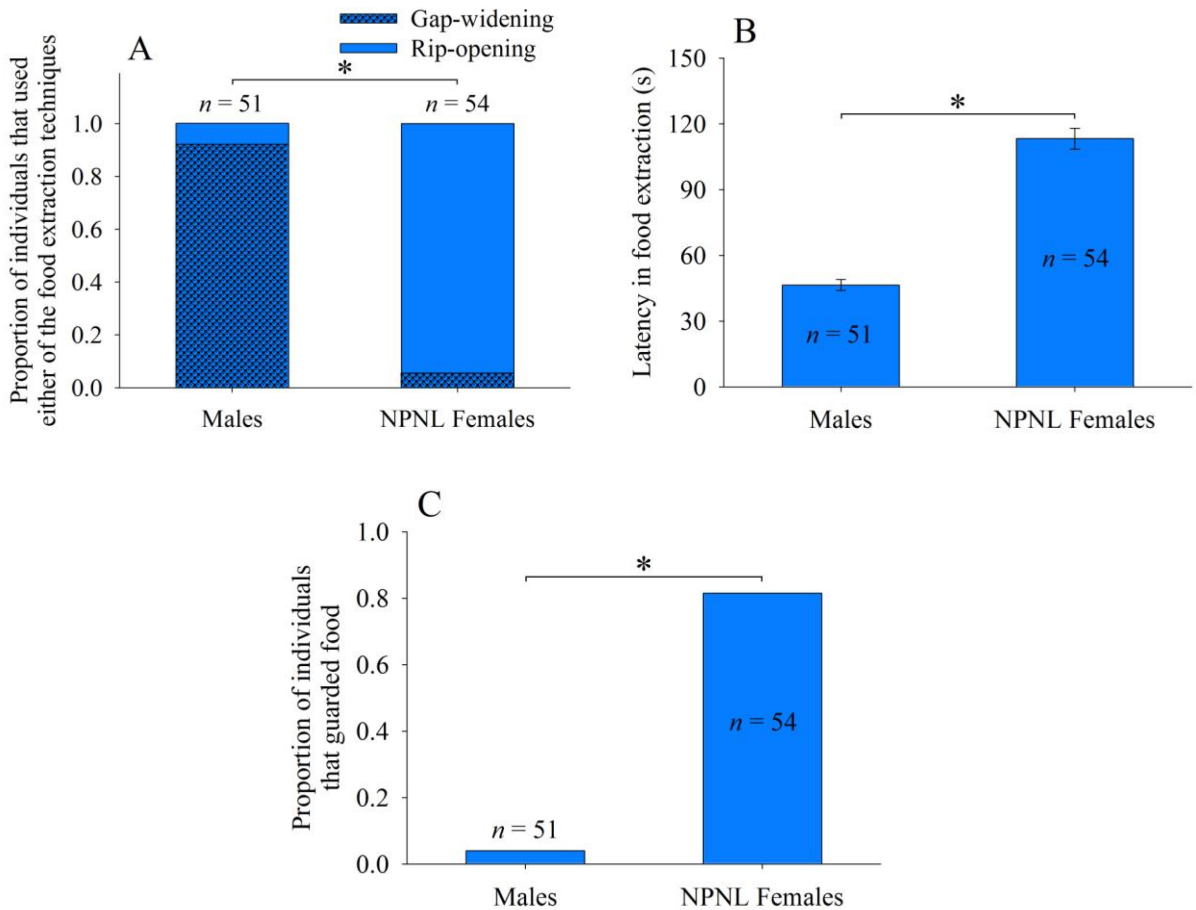


Figure 3. Food extraction behavior in stray dogs when presented with crafted food packets. Asterisks indicate significant differences. Error bars represent SE. (**A**) Males used gap-widening technique more frequently than NPNL females. (**B**) Males extracted food faster than NPNL females. (**C**) NPNL females guarded food more often than males.

Discussion

When provided with specially crafted food packets, it was typically the males that employed the gap-widening technique for food extraction (Figure 3A and Figure 3B). On the other hand, NPNL females used the less efficient rip-opening technique (Figure 3A and Figure 3B). Furthermore, NPNL females retreated to a secluded place before attempting extraction, whereas, males extracted food at the same time and place the packets were found (Figure 3C). These observations perhaps represent sex-specific differences in motivational states of animals with immediate ethological consequences. Male dogs are larger in size than female dogs (Lark et al., 2006). This may result in males having greater nutritional requirements and, therefore, adopting riskier strategies, that potentially have higher returns (here, risk refers to variability in expected returns), more often than NPNL females. Animals are known to exhibit intra-specific differences in foraging strategies when a risk taking strategy fetches greater returns for one individual over the other as it has been recorded in Indian elephants, *Elephas maximus indicus* (Sukumar and Gadgil, 1988), fallow deer, *Dama dama* (Appolonio et al., 2005), African buffalo, *Syncerus caffer* (Hay et al., 2008), and several primates species (Reader and Laland, 2001).

To investigate whether the use of the gap-widening technique was related to greater nutritional requirements, pregnant/lactating females were included as one of the groups in the subsequent study. Gestation and lactation raises the nutritional requirement in pregnant/lactating (PL) females (Gittleman and Thompson, 1998), possibly enhancing their motivation to maximize returns from foraging. PL females were therefore expected to perform differently from NPNL females in similar foraging tasks.

Experiment 2

Experimental procedure

Plasticboard food packets were presented to 64 naive dogs: 20 males, 24 NPNL females, 20 PL females, and given up to five minutes to open them (after which the packets were removed). There was no change, from the previous experiment, in the way the packets were presented. This process was repeated till an individual had extracted food using the gap-widening technique up to a maximum of three trials. Individuals were categorized into 'gap-wideners' or 'rip-openers' depending on their extraction technique. Gap-wideners were further presented with five learning trials with an inter-trial interval of one minute. Individuals were considered to have 'learned' the gap-widening technique if they extracted food in all five trials and used the gap-widening technique in at least four of them. A one-way ANOVA was used to find group differences among learners with latency in food extraction as dependent variable and group as categorical predictor. A repeated measure ANOVA was used to compare latency in food extraction over trials in learners and non-learners with latency in food extraction as dependent variable and group as categorical predictors. Appropriate statistical tests are indicated wherever required.

Results

Gap-widening technique proved superior to the rip-opening technique in terms of latency (Figure 4; independent samples t-test: $t_2 = -2.101$, $P = 0.038$) (comparison within NPNL females because of the rare use of the rip-opening technique in males and PL females).

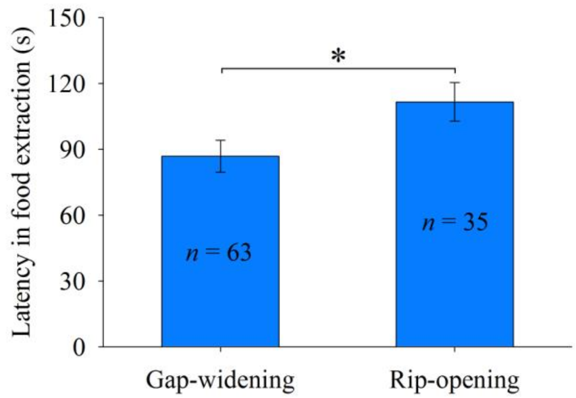


Figure 4. Gap-widening technique resulted in faster food extraction as compared to rip-opening technique. Asterisk indicates significant difference. Error bars represent SE.

As compared to NPNL females, males and PL females had higher proportions of gap-wideners (Figure 5A; multi-group proportions test: $\chi^2 = 11.502$, $P = 0.003$; for post-hoc analysis, see Table 1) and learners (Figure 5A; multi-group proportions test: $\chi^2 = 19.674$, $P < 0.001$; for post-hoc analysis, see Table 1). The latter guarded food more often than the former (Figure 5B; $\chi^2 = 16.727$, $P < 0.001$; for post-hoc analysis, see Table 1), used the two techniques arbitrarily and often failed in food extraction.

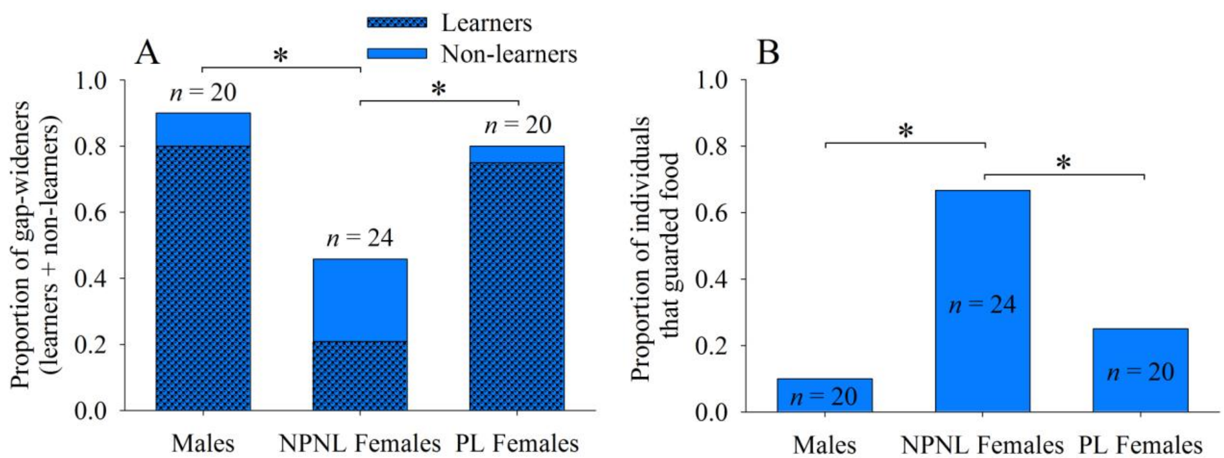


Figure 5. Food extraction and learning in stray dogs. Asterisks indicate significant differences.
(**A**) Compared to NPNL females, males and PL females had higher proportions of gap-wideners.
(**B**) NPNL females guarded food more often than males and PL females.

Table 1. Results of Marascuilo post hoc procedure.

Comparisons	Proportion of individuals that guarded food		Proportion of gap-wideners		Proportion of learners	
	χ^2	P	χ^2	P	χ^2	P
Males versus NPNL Females	23.338	< 0.001	13.141	< 0.001	23.538	< 0.001
Males versus PL Females	1.621	0.444	0.800	0.670	0.144	0.931
NPNL Females versus PL Females	9.317	0.009	6.364	0.041	18.059	< 0.001

Across all three groups learners behaved similarly (Figure 6A; one-way ANOVA: $F_{2, 33} = 0.353$, $P = 0.705$), extracted food faster than non-learners and improved with experience (Figure 6B; repeated measures ANOVA: $F_{1, 41} = 17.668$, $P < 0.001$, $n_1 = 36$, $n_2 = 9$; Tukey's HSD test: improvement within learners: 49.39%, $P < 0.001$).

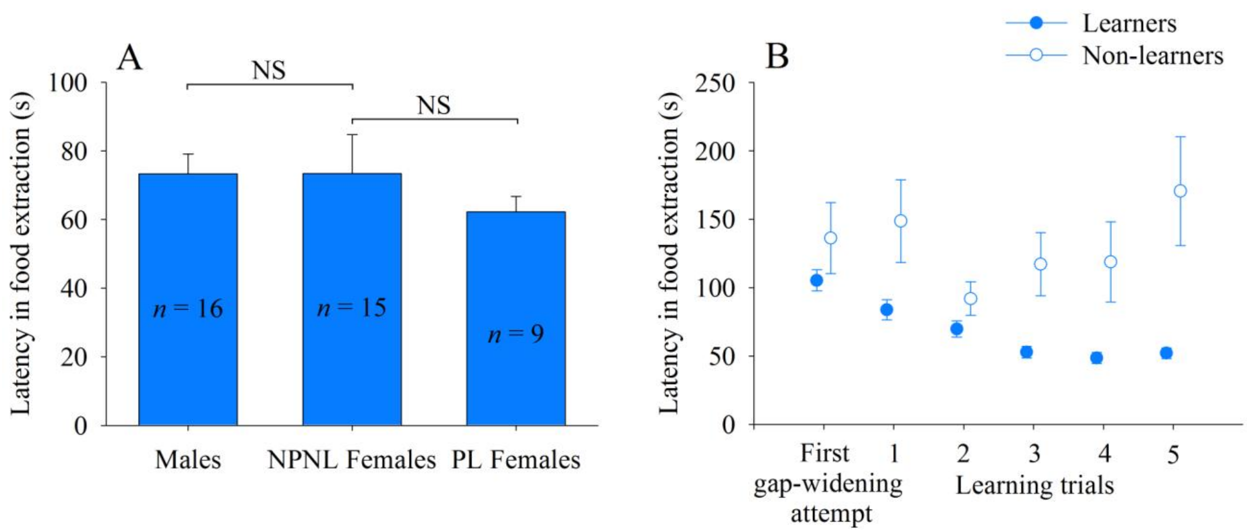


Figure 6. Learning process in stray dogs when presented with crafted food packets repeatedly. NS indicate non-significant differences. Error bars represent SE. (**A**) Learners did not differ across the groups. (**B**) Learners extracted food faster than non-learners and improved with experience.

Discussion

Males and PL females used the gap-widening technique repeatedly (Figure 5A) and improved with experience (Figure 6B). In contrast, NPNL females used either technique non-preferentially, with little or no improvement. We also observed that NPNL females typically retreated to a secluded place before attempting extraction, whereas, males and PL females, extracted food wherever the packets were found (Figure 5B). The use of the rip-opening technique always being accompanied with active food guarding together with NPNL females tending to rip open as compared to males and pregnant females, suggest that relatively greater nutritional requirements reduced risk aversion, which led to higher performance in males and PL females. The natural propensity of individuals to use risky strategies may be more contingent upon the physical conditions of an animal, and therefore a possible outcome of plastic behavioural adjustments wherein females behaved similar to the males during pregnancy/lactation.

Animals adopt riskier strategies when the returns compensate for potential risk (Krebs and Kacelnik, 1991; Lima and Dill, 1990; Ydenberg, 1998). Due to the pervasive nature of risk (here, risk refers to threat, i.e., hazards due to predation) , foragers apparently always remain vigilant (Ydenberg, 1998). Nevertheless, they can adjust their behavior to a perceived threat based on sensory information (Krebs and Kacelnik, 1991; Lima and Dill, 1990; Peckarsky et al., 1993; Ydenberg, 1998; Zanette et al., 2011). In the final study, the relationship between performance in the contexts of foraging and the direction of risk sensitive preferences in general was investigated. Dogs were presented with the same extraction task in a simulated high threat environment. Threatened individuals were anticipated to be more protective of their food sources by taking the packets to some safer place and perhaps increasing the time spent in vigilance by taking longer time in food extraction.

Experiment 3

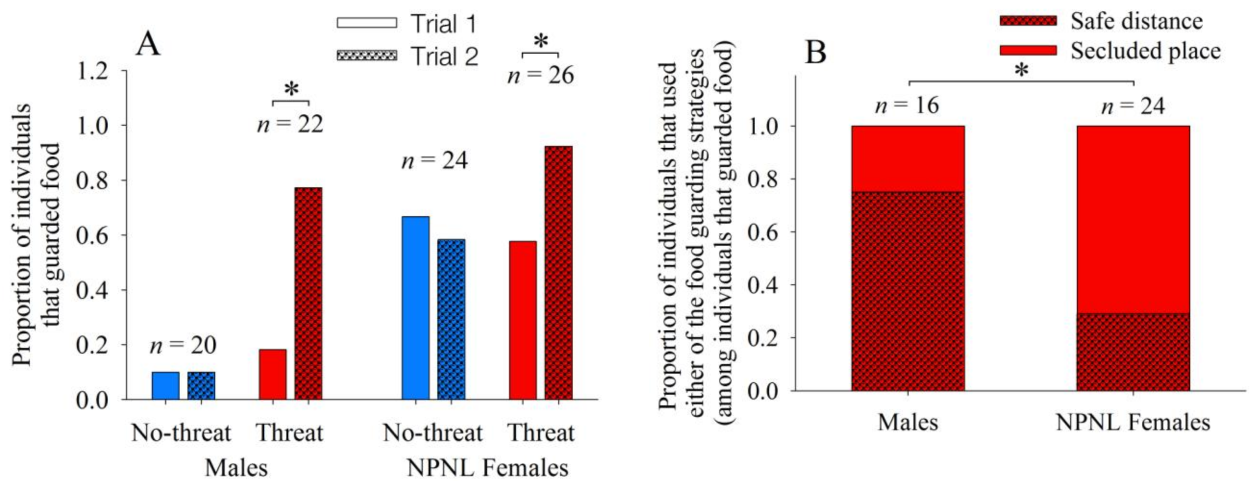
Experimental procedure

Plasticboard food packets were presented to 48 naive dogs: 22 males, 26 NPNL females and their extraction strategies were observed. They were then presented with a second packet and allowed to approach it. During the second trial, they were exposed to an artificial threat in the form of an approaching remote controlled car with flashing lights – the ‘attacker’ (Figure 7). The attacker was stopped as soon as subjects noticed it and started retreating. Threatened dogs typically returned after some time and took the packets to either a distant or a secluded place. The distance between each dog and the attacker at the time of retreat (flight initiation distance), the time before it returned to the packet, and the distance fled were recorded (Caro, 2005; Stankowich and Blumstein, 2005). Data obtained for males and NPNL females in the first two trials of the previous experiment was used as controls. General linear models (GLMs) were used to analyse the relationships between flight initiation distance, return time, and distance fled as dependent variable and group and the used extraction techniques as categorical predictors. Appropriate statistical tests are indicated wherever required.

Figure 7. The remote controlled car that was used as an attacker for threatening the dogs.

Results

As against the control, threatened individuals frequently guarded food (Figure 8A; males: threat: multi-group proportions test: $\chi^2 = 13.200$, $P < 0.001$; no-threat: $\chi^2 = 0.000$, $P = 1.000$; NPNL females: threat: $\chi^2 = 6.462$, $P = 0.011$; no-threat: $\chi^2 = 0.356$, $P = 0.551$); NPNL females retreated to a secluded place, whereas males maintained a safe distance from the attacker (Figure 8; multi-group proportions test: $\chi^2 = 8.087$, $P = 0.004$). After exposure to the threat, proportion of gap-wideners decreased in males (Figure 8; threat: multi-group proportions test: $\chi^2 = 4.539$, $P = 0.033$; no-threat: $\chi^2 = 0.125$, $P = 0.723$) but not in NPNL females (Figure 8; threat: multi-group proportions test: $\chi^2 = 0.746$, $P = 0.388$; no-threat: $\chi^2 = 2.277$, $P = 0.131$).



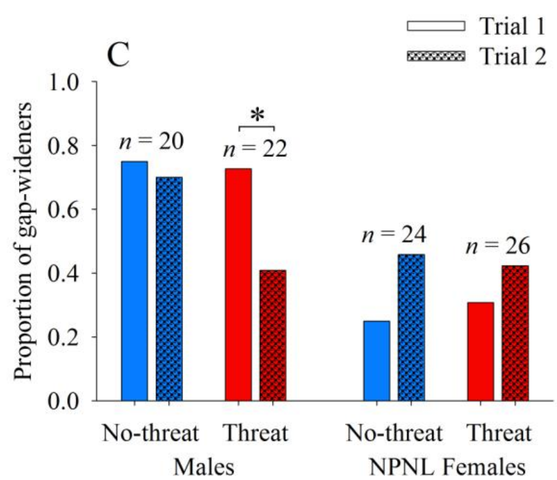


Figure 8. Food extraction behavior in dogs exposed to the attacker. Asterisks indicate significant differences. (**A**) Threatened individuals guarded food more often than unthreatened ones. (**B**) NPNL females retreated to a secluded place, whereas males maintained a safe distance from the attacker. (**C**) Proportion of gap-wideners reduced in threatened males but not in NPNL females.

Latency in food extraction increased after exposure to the threat (Figure 9A; males: independent samples t-test: $t_2 = -2.252$, $P < 0.032$, after removing '– 109' in no-threat condition, an outlier at $P < 0.05$; NPNL females: $t_2 = -2.680$, $P = 0.020$). Moreover, within gap-wideners, increase in latency for an individual was negatively correlated with its pre-threat latency in food extraction (Figure 9B; Spearman's rank correlation: $r_s = -0.608$, $n = 24$, $P = 0.002$).

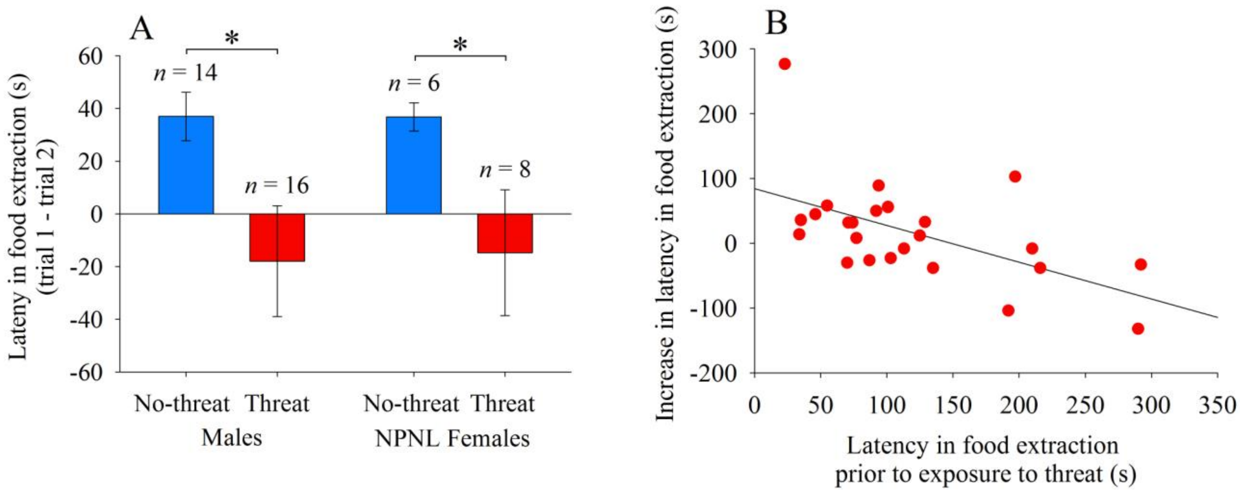


Figure 9. Effect of perceived threat on food extraction behavior in dogs exposed to the attacker. (**A**) Latency in food extraction increased in threatened gap-wideners but decreased in unthreatened ones. (**B**) Increase in latency for an individual was negatively correlated with pre-threat latency in food extraction for the same individual.

To eliminate effects of motivational differences (Cooper Jr. et al., 2006; Ydenberg, 1998), dogs that failed in food extraction in their first trial were excluded from further analysis. Compared to rip-openers, gap-wideners had a shorter flight initiation distance (Figure 10A; $F_{1, 36} = 10.099$, $P = 0.002$). Although flight initiation distance did not differ between the sexes (Figure 10B; $F_{1, 36} = 0.047$, $P = 0.830$), the difference was larger between gap-wideners and rip-openers in males than in NPNL females (Figure 10C; $F_{1, 36} = 4.045$, $P = 0.052$).

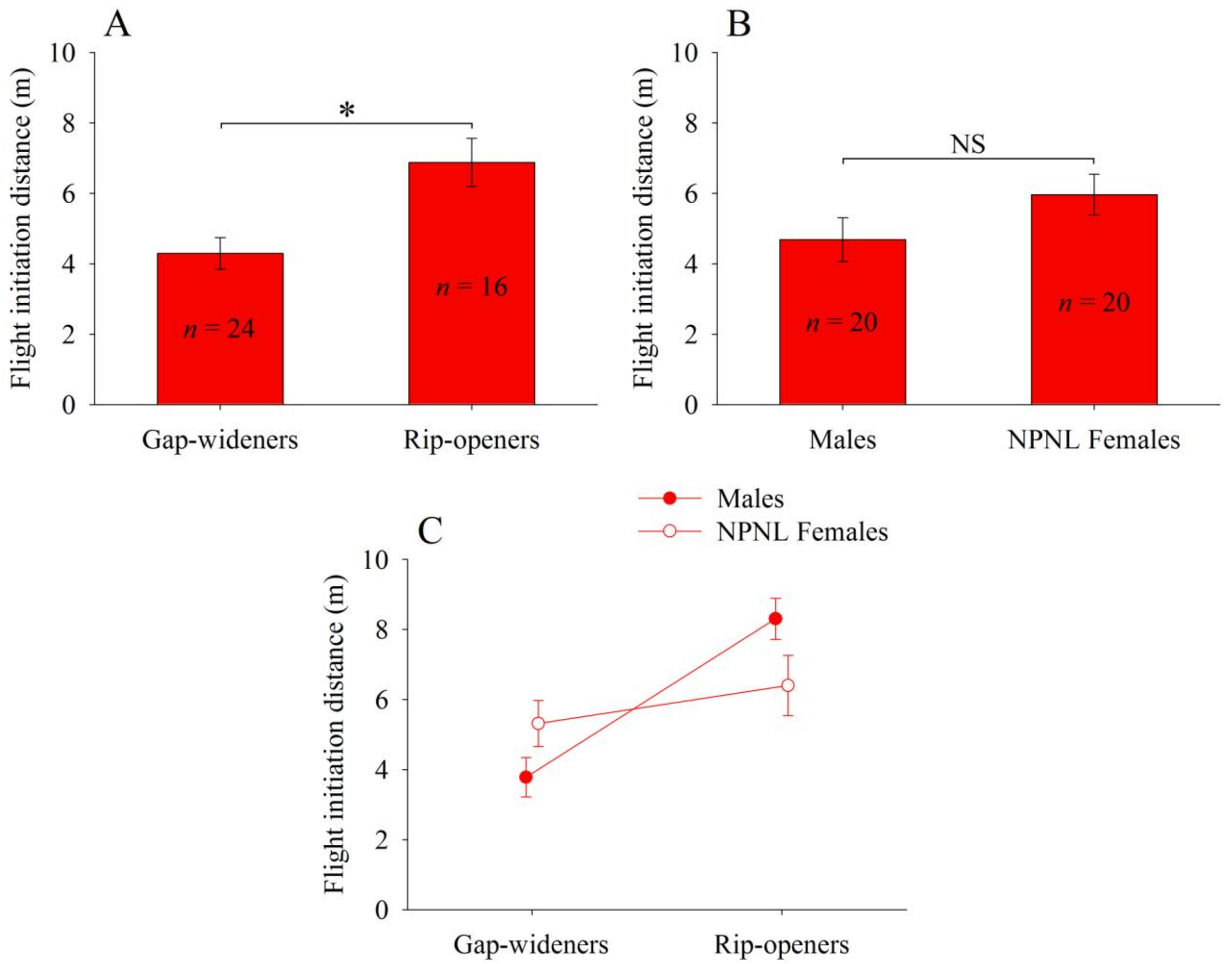


Figure 10. Flight initiation distance in dogs exposed to the attacker. Asterisk and NS indicate significant and non-significant differences respectively. Error bars represent SE. (**A**) Gap wideners had smaller flight initiation distance compared to rip-openers. (**B**) Flight initiation distance did not differ across the sexes. (**C**) Difference in flight initiation distance was larger between gap-wideners and rip-openers in males than in NPNL females.

Gap-wideners returned to the packets earlier than rip-openers (Figure 11A; $F_{1, 36} = 20.513$, $P < 0.001$). Although return time did not differ between the sexes (Figure 11B; $F_{1, 36} = 3.697$, $P = 0.624$), the difference was larger between gap-wideners and rip-openers in males than in NPNL females (Figure 11C; $F_{1, 36} = 5.800$, $P = 0.021$).

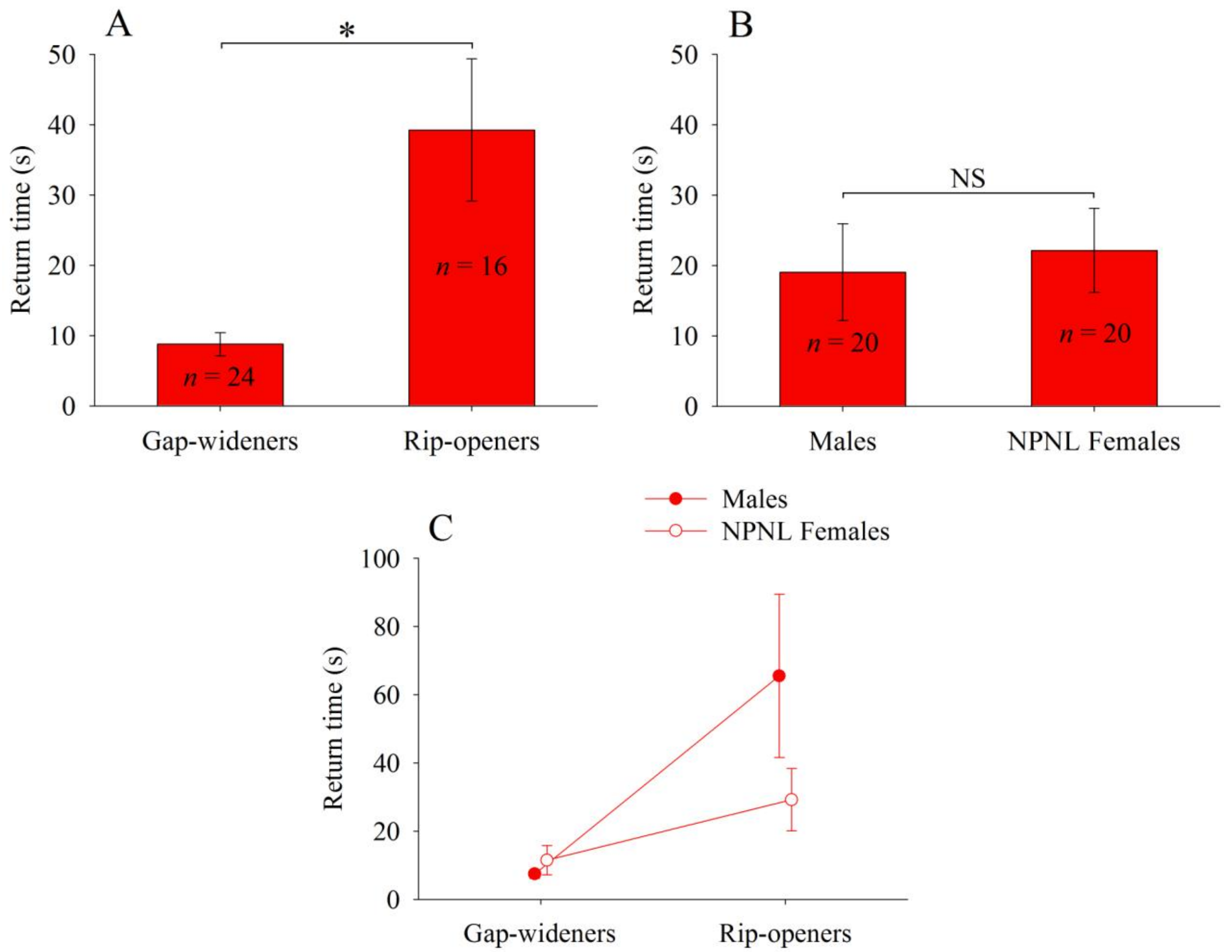


Figure 11. Return time in dogs exposed to the attacker. Asterisk and NS indicate significant and non-significant differences respectively. Error bars represent SE. (**A**) After exposure to the attacker, gap wideners returned to the packets earlier than rip-openers. (**B**) Return time did not differ across the sexes. (**C**) Difference in return time was larger between gap-wideners and rip-openers in males than in NPNL females.

Compared to rip-openers, gap-wideners fled with the packets to a shorter distance (Figure 12A; $F_{1, 36} = 13.092$, $P < 0.001$). Although distance fled did not differ between the sexes (Figure 12B; $F_{1, 36} = 2.375$, $P = 0.132$), the difference was larger between gap-wideners and rip-openers in males than in NPNL females (Figure 12C; $F_{1, 36} = 7.493$, $P = 0.001$).

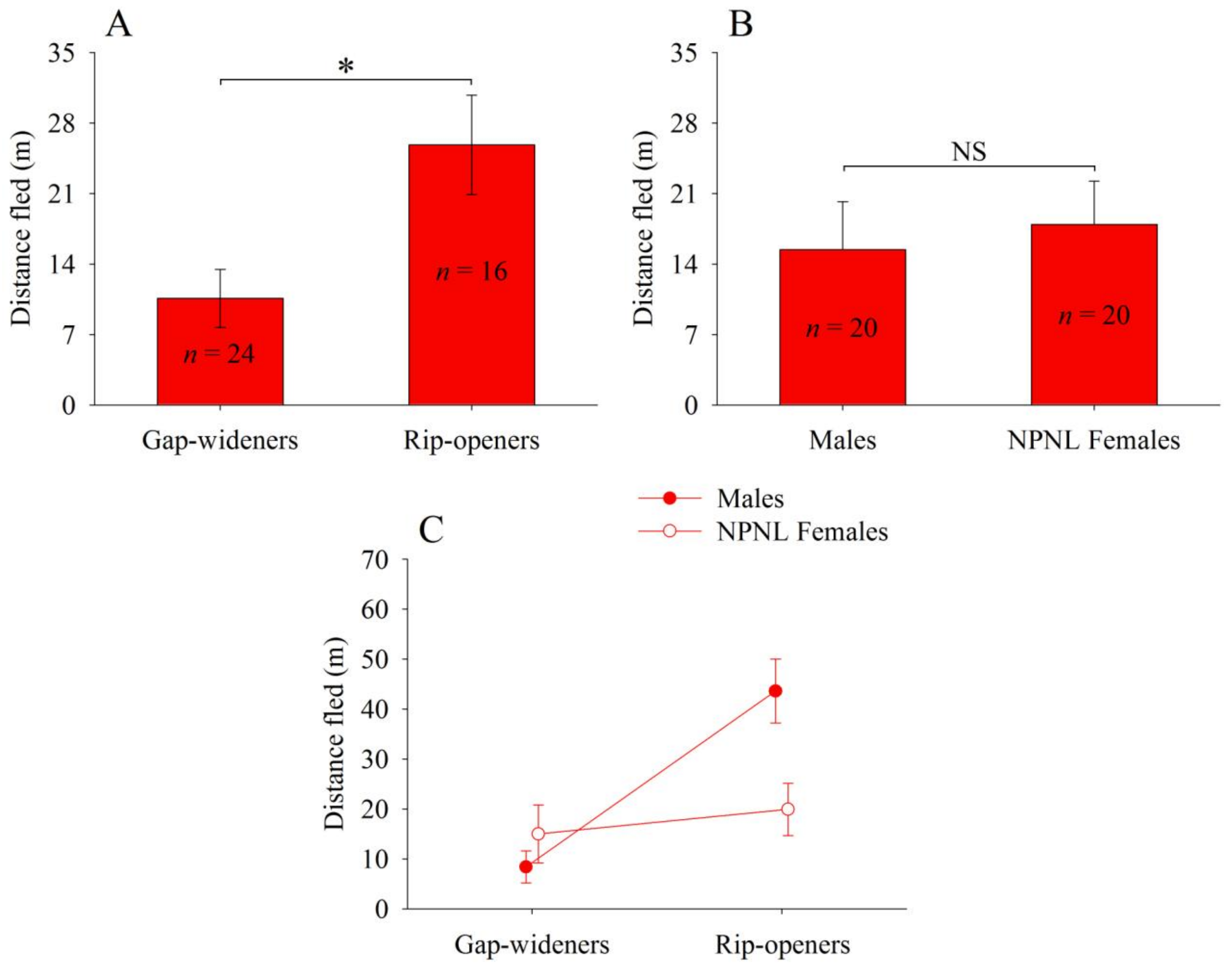


Figure 12. Distance fled in dogs exposed to the attacker. Asterisk and NS indicate significant and non-significant differences respectively. Error bars represent SE. (**A**) Gap wideners fled with the packets to a smaller distance than rip-openers. (**B**) Distance fled did not differ across the sexes. (**C**) Difference in distance fled was larger between gap-wideners and rip-openers in males than in NPNL females.

Moreover, within gap-wideners, latency in food extraction was positively correlated with flight initiation distance (Figure 13; Spearman's rank correlation: $r_s = 0.705$, $n = 24$, $P < 0.001$).

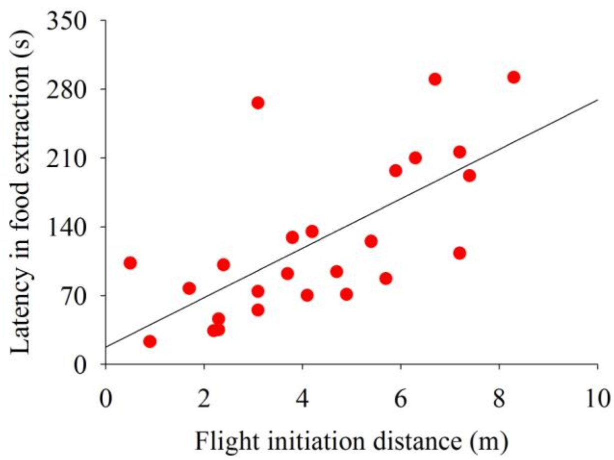


Figure 13. Latency in food extraction was positively correlated with flight initiation distance within threatened gap-wideners

Discussion

Perception of threat resulted in changes in behavior that negatively affected foraging performance (Figure 8 and Figure 9A), perhaps due to increased time spent in vigilance (Lima and Dill, 1990). Perceived threat has been shown to reduce activity, growth, and fecundity in animals (Peckarsky et al., 1993; Zanette et al., 2011). The observed differences in the food guarding strategies between males and females (Figure 8B) once again indicate sex-differences in risk aversion; females being more averse to risk (here, ‘risk’ refers to predation hazards and not necessarily variation in expected returns) than males in general. The negative relationship between increase in latency for an individual and pre-threat latency in food extraction for the same individual (Figure 9B) suggest that individuals with higher foraging performance are more sensitive to a threatening situation, i.e. already being near their peak, have performance suffer.

Individuals with higher foraging performance were less fearful to perceived threats measured in terms of flight initiation distance, return time, and distance fled (Figure 10, Figure 11, and Figure 12) (Caro, 2005; Stankowich and Blumstein, 2005) with a negative relationship between performance and fearfulness at the level of an individual (Figure 13). Together, these observations demonstrate how foragers may combine information from different sources to estimate the likelyhood of the presence of a predator and take the appropriate foraging decisions.

General discussion

Considerable intra-specific differences were observed in foraging performance, which were quantitatively measured as shorter latency in food extraction (Figure 3B and Figure 4A) and qualitatively measured as performance in a relatively sophisticated technique (Figure 3B and Figure 5A) that improves with experience (Figure 6). Males performed better than females that used a less efficient extraction technique and actively guarded food (Figure 3, A to C and Movie S2). Additionally, during pregnancy/lactation, females behaved similar to the males wherein they used the gap-widening technique and attempted extraction wherever they found the packets (Figure 5, A and B). Together, these observations suggest that relatively higher nutritional requirements in males and PL females (Gittleman and Thompson, 1998; Lark et al., 2006; Pal, 2005) reduced risk aversion that resulted in higher foraging performance.

Animals forage in diverse environments, making a particular set of strategies unlikely to be universally applicable. Our study thus outlined a general framework to understand the interaction between different kinds of information that may influence foraging decisions. Foragers used strategies that differ in the associated risk and returns; perhaps the rip-opening technique allows better vigilance than the gap-widening technique (Movies S1, 2) but results in less efficient food extraction (Figure 3 and Figure 4). Food guarding reduces the chances of losing the food to a competitor. Threatened dogs were found to switch their extraction strategies (Figure 8 and Figure 8C) that led to lower foraging performance (Figure 9A). High performers were more sensitive (Figure 9C) and less fearful (Figure 10, Figure 11, and Figure 12) to perceived threats, and importantly, at the level of an individual (Figure 9B and Figure 13). Collectively, these observations indicate a complex underplay of cognitive mechanisms in the contexts of foraging and risk evasion.

Although the observed gap-widening technique may not be labeled as an 'innovation', conditions in natural habitats similar to those created in our experiments could actually be the triggers of 'creativity' or cognitive capabilities in animals (Kummer and Goodall, 1985; Lee, 2003). Future research, therefore, needs to integrate the evolutionary, ecological, and cognitive aspects of behavior while studying foraging processes. This will help to elucidate whether risky strategies are largely the products of direct selection acting on the fitness consequences of foraging in resource scarcity or they are the products of selection for cognitive mechanisms that underlie a broader repertoire of behavior.

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Supplementary material

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Movie S1. This footage shows a male stray dog using the gap-widening technique of food extraction. The animal uses its forelimbs to hold the packet vertically against the ground, widens the space enclosed between the two flaps of the packet, and pulls out the chicken claw with its mouth.

Movie S2. This footage shows a female stray dog using the gap-widening technique of food extraction. The animal firmly holds the packet between its forepaws and the ground, and rips it open with its mouth.