ORIGINAL ARTICLE

Stranger Danger: Differential response to strangers and neighbors by a social carnivore, the Asiatic wild dog (*Cuon alpinus*)

Pallavi Ghaskadbi[1] · Parag Nigam[1] · Bilal Habib[1]

Abstract
The function of holding territories is primarily to have access to resources like food and mates. However, it is costly in terms of energy and time investment. Solitary-living, territorial species are known to reduce these costs by being more aggressive towards unfamiliar strangers and less aggressive towards neighbors. However, in social, territorial species, neighbors can impose a greater threat than strangers. We tested whether the highly social Asiatic wild dogs/dholes (*Cuon alpinus*) exhibit the "nasty neighbor" or the "dear enemy" phenomena in Tadoba Andhari Tiger Reserve (TATR), Maharashtra, India. We conducted scat translocation experiments where we presented fresh scats collected from unique donor groups to a resident dhole group and tested the type and the intensity of behavioral response (duration) to the stimulus. Dholes responded differentially to the two treatments suggesting they exhibit neighbor-stranger discrimination. Overall, strangers elicited a stronger response with longer duration and larger packs were less likely to respond to the stimulus than smaller packs. Differences found between categories of dhole scent marks establish the importance of olfactory communication, especially "counter-marking" in the species. Within recipient packs, individual status affected the response to trials wherein the alpha pair reacted more intensively to strangers than others. Our study provides experimental evidence to demonstrate that dholes exhibit the "dear enemy" phenomenon.

Significance statement
Animals defend territories from other members of their own species, but intrusions are commonplace in the wild. Different intruders may pose different levels of threats, and hence, intruders are treated differentially to minimize the energetic costs of territorial defense. In some animals, neighbors with well-established territories may become less aggressive towards each other. This is known as the dear enemy effect. By contrast, at times neighbors may represent a greater threat than strangers which is known as the "nasty neighbor" effect. We experimentally show that dholes exhibit the dear enemy phenomenon by responding more intensively to strangers than familiar neighbors. We show how response varied based on hierarchy in a pack as well as the pack sizes. Furthermore, we found that, both in core as well as buffer areas of their own territory, this relationship was consistent.

Introduction

Territoriality may be defined as the defense of a fixed physical space against conspecifics (Maher and Lott 1995; Darden and Dabelsteen 2008) and is observed across various taxa. Defended areas may contain resources such as foraging sites, dens or nests, or sexual partners. Territoriality mediates competitive intraspecific interactions and is a complex interplay between social and ecological factors (Brown and Orians 1970; Maher and Lott 2000). Territories may be defended actively in the form of aggressive physical combats with intruders or passively via the signaling of auditory, olfactory, and visual cues (Gese 2001). In either form, territorial defense is costly in terms of time, energy, risk of predation, and/or injury (Brown 1964; Temeles 1994; Ydenberg et al. 1988), specifically for social animals (Taborsky et al. 2005). Evidence suggests that in social animals with a single breeding pair, other members or "helpers" may pay costs in terms of reduced growth and future reproductive ability (Taborsky

✉ Bilal Habib
  bh@wii.gov.in

[1] Department of Animal Ecology and Conservation Biology, Wildlife Institute of India, Dehradun 248001, Uttarakhand, India

1984; Balshine-Earn et al. 1998; Kokko et al. 2002; Bergmüller et al. 2005), risky or energetically costly helping behavior (Taborsky and Grantner 1998; Balshine et al. 2001), and costs of contributing to territorial defense (Nunn and Deaner 2004).

Canids are a diverse group of mammals that display a great variation in terms of their distributions and social systems along with a range of behavioral plasticity (Macdonald et al. 2019). The consequent diversity exhibited in the models of territoriality among wild canids, between and within species, has been demonstrated previously, but observations of direct confrontations for territorial defense have been limited (Camenzind 1978; Bekoff and Wells 1986; Mech 1993, 1994; Jordan et al. 2017). Since direct confrontations involving chases or physical fights are costly in terms of time and energy, they are usually utilized as a last resort when an outcome has not been reached by less costly means (Hardy and Briffa 2013; Christensen and Radford 2018). Subsequently, indirect mechanisms of territorial maintenance and defense like scent marking, howling, or a combination of the two have been comprehensively documented in species like wolves *Canis lupus* (Peters and Mech 1975; Rothman and Mech 1979; Harrington and Mech 1978a, b, 1979, 1983; Harrington 1987), coyotes *Canis latrans* (Camenzind 1978; Barrette and Messier 1980; Bowen and Cowan 1980; Gese and Ruff 1997, 1998; Gese 2001), Ethiopian wolves *Canis simensis* (Sillero-Zubiri and Macdonald 1998), and African wild dogs *Lycaon pictus* (Parker 2010). Although scent marks are intended to ward off intruders, in the wild, intrusions are a common phenomenon. However, not all intruders pose similar risks to the residents. Therefore, it is energetically optimal for animals to discriminate among the nature of intruders and respond accordingly (Jaeger 1981).

An economic strategy by which defense costs may be lowered is to exhibit reduced aggression towards familiar occupants or neighbors than towards non-neighbors (strangers) and is known as the "dear enemy" phenomenon (Fisher 1954; Temeles 1994). The dear enemy phenomenon draws from two other hypotheses—the familiarity hypothesis (Ydenberg et al. 1988) and the threat level hypothesis (Temeles 1994). The familiarity hypothesis suggests that the residents' familiarity to neighbors reduces the likelihood of conflict as opposed to unfamiliar strangers, and the threat level hypothesis suggests that residents respond strongly to strangers as they may pose a greater threat to resources than neighbors. Identifying neighbors is one of the most widespread forms of social recognition among animals. Territorial animals are known to avoid the costs incurred in repeated aggressive interactions with conspecifics that pose little threat to their territorial ownership by recognizing established neighbors. Conversely, at times, the response to neighbors is more intense than the response to strangers. Müller and Manser (2007) described the "nasty-neighbor" phenomenon in banded mongooses *Mungos mungo* with intense competition between neighbors compared to non-neighbors (hereafter strangers). The nasty-neighbor phenomenon may be observed in social

animals wherein familiar neighbors pose a higher risk than non-familiar strangers, whereas fleeting strangers may be outnumbered by residents and pose a lower threat (Müller and Manser 2007) as potential usurpers of territories, opponents in lethal fights, and competitors for resources like mates or food. Theoretically, social territorial species would tend to exhibit the nasty-neighbor phenomena since the chances of stranger groups taking over resident territories are less as compared to a group of neighbors. Based on our observations of dholes in the study area, strangers tend to be individual dispersers (not groups) from non-neighboring packs, therefore may pose a less of a threat than neighbors (groups). Such an escalated response to neighbors over strangers has been previously demonstrated in social territorial species across various taxa like the mammals (banded mongoose, Müller and Manser 2007; striped mice *Rhabdomys pumilio*, Schradin et al. 2010), birds (chowchilla *Orthonyx spaldingii*, Koetz et al. 2007), insects (weaver ants *Oecophylla smaragdina*, Newey et al. 2010) and fishes (Bruintjes et al. 2016).

Asiatic wild dogs or dholes are endangered, highly social carnivores found in South and South East Asia (Johnsingh 1982; Kamler et al. 2015). Among the most social of all carnivores, individual dholes cooperate to feed and guard litters of pups, hunt, and defend their large territories in packs of up to 30 or more individuals (Johnsingh 1982; Durbin et al. 2004). In the past, behavioral studies on dholes have been mostly conducted through ad libitum data collection methods (Johnsingh 1982; Venkataraman et al. 1995; Karanth and Sunquist 2000). There is a limited understanding of the behavioral ecology of dholes, especially in terms of quantitative studies of inter and intrapack interactions in the wild (Johnsingh 1982; Ghaskadbi et al. 2016; Bhandari et al. 2021).

Dholes display characteristic scent-marking behaviors (Johnsingh 1980, 1982; Ghaskadbi et al. 2016), suggesting that olfactory communication is of paramount importance in the social species. With this background, we set out to systematically test whether a social territorial carnivore like the dhole, discriminated between conspecific neighbors and strangers. We conducted scat translocation experiments wherein we placed scent marks from neighboring and non-neighboring groups in a resident pack's territory and recorded their type and intensity of response. Specifically, we investigated whether dhole packs exhibit the "dear enemy" or the "nasty neighbor" phenomena in their social interactions and what factors affect their response to foreign scents from other packs.

Methodology

1) Study area

The Tadoba Andhari Tiger Reserve (20°04′53″ to 20°25′5″ N and 79°13′13″ to 79°33′34″ E) is a 1700 km² protected area located in the Chandrapur district of the

state of Maharashtra, India. Tadoba-Andhari Tiger Reserve (TATR) is considered one of the key source populations for tigers (*Panthera tigris)* in Central India. This region also supports a critical population of dholes and is one of the remaining strongholds of the species in the Central Indian Landscape. The TATR comprises of the Tadoba National Park spread over an area of 116.55 km^2 and the Andhari Wildlife Sanctuary spread over 508.85 km^2 (Fig. 1). This biodiverse region includes 41 species of mammals, more than 195 species of birds, 111 species of butterflies, and 30 species of reptiles (Nagendra et al. 2006; Habib et al. 2020). The intensive study area is the 625.40 km^2 core area of the TATR. This area can be characterized as a southern tropical dry deciduous forest (Champion and Seth 1968). The tiger, leopard (*Panthera pardus*), and the dhole are the large carnivores found in the study area. Other carnivores include sloth bear (*Melursus ursinus)*, jungle cat (*Felis chaus*), palm civet (*Paradoxurus hermaphroditus*), small Indian civet (*Viverricula indica*), ruddy mongoose (*Herpestes smithii*), common mongoose (*Herpestes edwardsi*), and ratel (*Mellivora capensis*). The prey base of carnivores comprises of species like the chital (*Axis axis*), sambar (*Cervus unicolor*), nilgai (*Bosephalus tragocamelus*), gaur (*Bos gaurus*), wild pig (*Sus scrofa*), chausinga (*Tetracerus quadricornis*), Barking deer (*Muntjacus muntjak*), the common langur (*Semnopithecus entellus*), black-naped hare (*Lepus nigricollis*), and Indian porcupine (*Hystrix indica*). The reserve has 2 villages in the core and 79 villages in the buffer zone. The buffer zone is composed of villages, agricultural land, and a wide array of recreational facilities for tourists.

2)   Sample collections and scat translocation trials

We identified 8 unique dhole packs in the Tadoba Andhari Tiger Reserve from 2016 to 2018 as a part of a long-term monitoring program by direct observations and camera trapping. As dholes lack distinct, identifiable patterns on the coats, conspicuous features like injury marks, or unusual color patterns of one/multiple pack members were used to assign identity to the packs. Following the identification in field, 5 individuals from four packs were radio-collared to study the space use and behavioral ecology of the little-known dhole. We then derived the home range, buffer, and core based on radio-telemetry data (PG et al. unpubl. data). All dholes were fitted with GPS radio collars (Vectronics, Berlin, Germany) with a UHF (ultra-high frequency) ground download system. We computed the home ranges by using the kernel density estimator (KDE) (Worton 1989; Borger et al. 2006). KDE uses non-parametric analysis to create a utilization distribution that describes the probability of an animal to be present at a location (Worton 1989). We defined home range for each dhole as the area containing 95% of the estimated utility distribution and area of intensive use "core areas" as 50% of

the estimated utility distribution (Worton 1989; Seaman and Powell 1996). The home range analyses were performed in ArcGIS 10® (ESRI) and ArcGIS Pro (ESRI) using Home Range Tools V.3.27 (Rodgers et al. 2007) extension.

For each scat translocation trial, we collected 3–5 samples of fresh dhole scat from a donor group by following them in field on foot or by vehicles. The scats were considered fresh until they were dry and had no apparent moisture (up to 24–48 h). We collected all the samples of scats on the field from known packs in the wild, and no animals were captured to collect scats. We used Ziploc bags to collect fresh samples and store them in a dry place in cool boxes. We presented all experimental groups with 3 samples during each individual trial consistently throughout the entire study. We selected 3 scat samples (per experiment) as our presented stimulus based on the number of individuals in the smallest pack size in the area. The scats were placed on the trails or roads as a pack was seen approaching. As dholes have been observed to scent mark at communal latrine sites, primarily at junctions where two or more trails meet (Johnsingh 1980; Ghaskadbi 2015), we placed the scats together to match a natural latrine site. Each trial consisted of 4 treatments: neighbors, a non-neighboring group ("strangers"), own ("control 1"), and a blank soil sample ("control 2"). The soil for control 2 was collected from the territory of the experimental pack and was standardized across all trials with uniform sample weights. The "neighbor" scats were from identified/radio-collared neighbor packs, whereas the "stranger" scats were from identified packs from the TATR buffer and other forested areas from the same landscape (Supplementary 3). For each scat translocation trial, samples were arranged on open ground with no/minimal undergrowth or on blacktop roads. No baits were used to direct or lure the dhole packs to the stimuli. We made all the observations from vehicles at a distance of 10–50 m with minimal disturbance and recorded the number and duration of responses to the presented scat samples. A pro-zoom video camera (Canon SX60 model) was used to record the experiments for later analysis. We waited for a pack to respond to the provided stimulus until the packs had left the trial site and were no longer visible. We presented the scats of unique donor groups in separate trials at different locations, i.e., from the buffer and the core of an experimental group's territory. We excluded the pup scent marks from the experiments. The control and treatment trials were randomly carried out (in no particular order), and experiments on the same group were spaced at least 14 days apart to minimize carry-over effects.

Type of response

We recorded the response of the recipient group in three groups based on the hierarchy of the pack viz. alpha male (AM), alpha female (AF), and others (other non-breeding
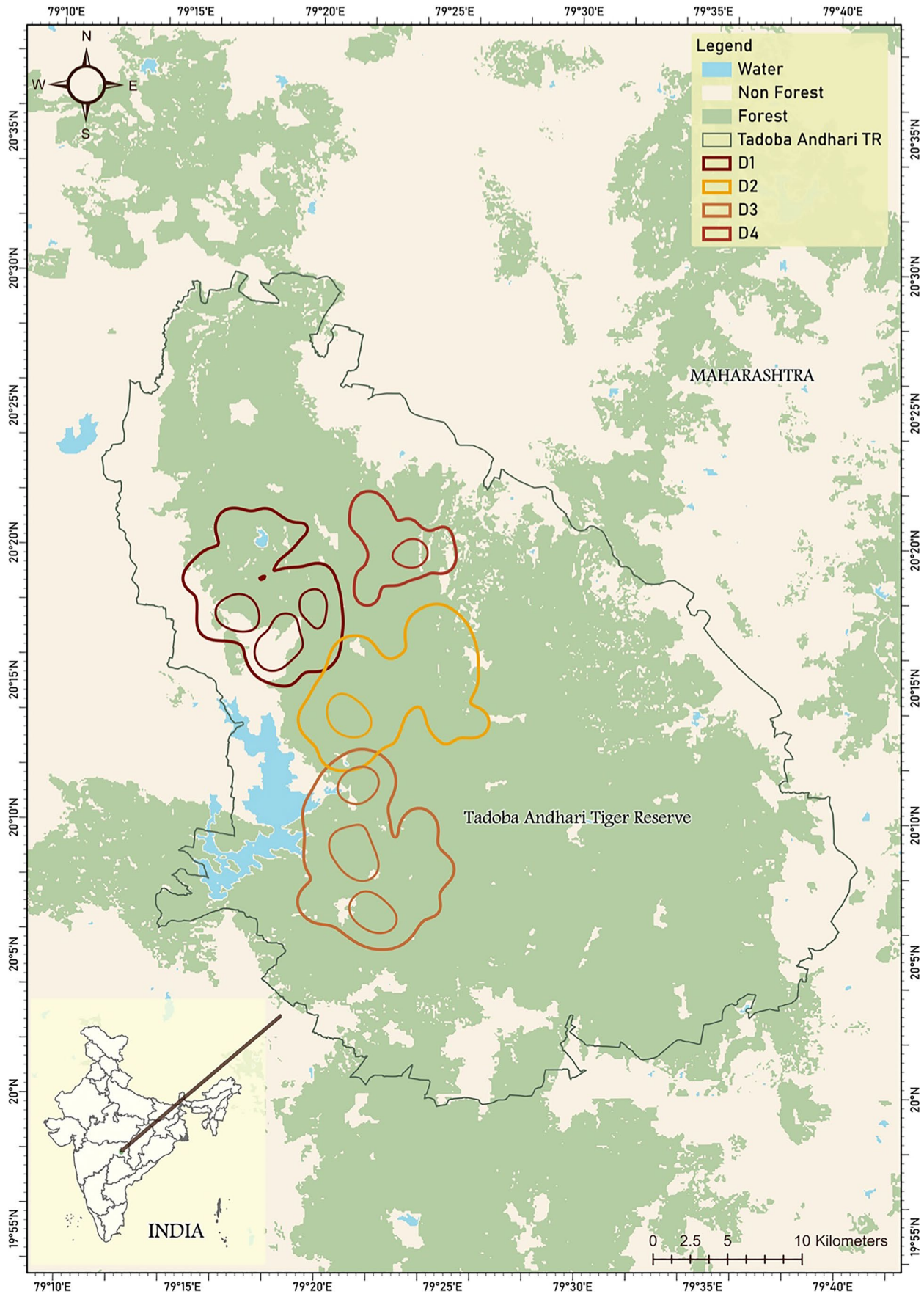
◀**Fig. 1** A forest cover map of the Tadoba Andhari Tiger Reserve with home range boundaries (95%) and intensive use areas or "cores" (50%) within the ranges of experimental dhole packs using kernel density estimators (KDE), Maharashtra, India

pack members). The responses of only adult pack members were included as pups may not recognize neighbors and strangers (Müller and Manser 2007). The dominant pair (alpha male and female) was distinguished from the rest of the pack members by the color of their coats (white chest, legs, and lips) that becomes prominent in the breeding season and other pair-bonding behaviors (Ghaskadbi et al. 2016). Focal sampling was done to record the responses of pack members (Lehner 1998). We did not blind record data as our study involved focal animals in the field. To study the response of dholes to the experiment/donor scat, we recorded 3 types of responses based on reviewing the literature on dholes (Ghaskadbi et al. 2016) and other similar experiments (Müller and Manser 2007; Parker 2010).

1) Inspection bout (IB): The recipient approaches and sniffs the scat presented.
2) Inspection bout + counter-mark (IB, CM): the recipient approaches and sniffs the scat, followed by a urination event either on top/adjacent to the presented scat.
3) Inspection bout + worry calls (IB, WC): the recipient approaches and sniffs the presented scat, followed by "yelping" at the other pack members.

Intensity of response

The intensity of the response was measured in terms of the duration of the response, wherein we considered the longer the duration of a response, higher was its intensity. The duration of inspection bouts (one individual inspecting one sample) was determined frame-by-frame in iMovie (ver. 10.1.8) in seconds. We recorded the response of a focal animal from the time it started a directional approach towards the presented sample until it stopped inspecting the sample and started moving away (Parker 2010). The directional approach was generally observed within a radius of ~5 feet of the presented scat samples.

3) Data analysis

We recorded a total of ~30 min of responses over 200 scat translocation trials in the wild. We conducted all statistical analyses and plots in the R programming language (R Studio Team 2020) (Supplementary 2). First, we investigated whether the dholes responded differentially to the control trials–own ($n = 41$) or soil samples ($n = 21$) versus the treatments–neighbor ($n = 55$) or stranger samples ($n = 60$). We utilized generalized linear mixed models

(GLMM) with response to a trial as a dependent variable (0, no response; 1, response) with a binomial error distribution. The two response types—IB and IB + CM—were pooled as "response" for the analyses. Previous work on social canids indicates that familiarity, pack hierarchy, and spatial context of the resident pack might affect responses towards conspecifics (Parker 2010). Therefore, we included scat origin (own, soil, neighbor, stranger), responder (alpha male, alpha female, or other pack members), region of dhole home range (core, buffer), and pack size as independent variables or fixed effects in each model. Additionally, we used pack identity as a random variable for the analysis to control for repeated measures.

After establishing the differential probability to respond to controls and treatments, we subsequently investigated whether the intensity of response (measured as the duration in seconds) to the two treatments—neighbor and stranger differed significantly. We used a subset of the data for this analysis to identify the important variables and interactions between the two treatments explicitly. We used scat origin (own, soil, neighbor, stranger), responder (alpha male, alpha female, or other pack members), region of recipient dhole home range (core, buffer), pack size, and their plausible ecological interactions as independent variables (Table 1). We also used pack identity as a random variable for the analysis. Similar to GLMM 1, the two response types—IB and IB + CM—were pooled as "response duration."

We first ran a global model with all the variables and their interactions using the R package "glmmTMB" (Magnusson et al. 2017). Following Anderson and Burnham (2002), we created ecologically meaningful models with predictors based on our knowledge of dholes in the study area. We then used model averaging for models with ΔAIC < 2 (Arnold 2010) to get the most parsimonious model. Our null hypothesis was that the dholes would not respond differentially to neighbor and stranger scats.

Results

Type of response

We conducted a total of 200 scat translocation trials, out of which 178 were analyzed. From the 3 types of responses that were recorded, we found that Inspection bouts + counter-marking (IB + CM) was the most common type of response followed by inspection bouts (IB). We also recorded a single event of inspection bout + worry call (IB + WC); however, we did not include it in our analysis. We found that dholes inspected and counter-marked (IB + CM), 81.74% ($n = 94$) of the treatment samples compared to only 15.87% ($n = 10$) of the control samples

Table 1 Description of variables and interactions between variables used in the generalized linear mixed models arranged serially (Sr. No.)

Sr. No	Variable	Range/levels
1	pack.size	3–12
2	core.buffer	Core
		Buffer
3	Responder	Alpha male
		Alpha female
		Others
4	scat.origin	Neighbor
		Stranger
		Soil
		Own
Interactions		
1	scat.origin *core.buffer	
2	scat.origin * responder	
3	scat.origin *pack.size	
4	core.buffer * pack.size	
5	core.buffer * responder	

Fig. 2 Response of dholes to different donor groups in the scat translocation experiments, Tadoba Andhari Tiger Reserve, India. The response NIL, no response; IB, inspection bout; and IB + CM, inspection bout + counter-marking. The control includes control 1 and control 2 (soil and own scats) and the treatment includes "strangers" and "neighbors"

(Fig. 2). In all, 35 trials did not elicit any response from the dhole packs of which 33 were controls. Following this preliminary analysis, we conducted our main analyses following a two-step process.

Intensity of response

First, we established that the response probability to controls was significantly different than the treatments (GLMM1). Our results suggested that the probability to respond to own and soil samples was significantly less (own: -3.94; 95% CI $= -6.11$ to -1.78; $p < 0.001$), (soil: -5.46; 95% CI $= -7.82$ to 3.11; $p < 0.001$) than to neighbors and strangers (Fig. 3, Tables 2 and 3) suggesting that dholes could differentiate between conspecific scents and their own/soil scent. The generalized linear mixed model results also suggested that the probability of responding to the stimulus decreased significantly as pack size increased (0.23; 95% CI $= -0.40$ to -0.06; $p < 0.01$) (Table 3, Supplementary 4).

Subsequently, the findings from GLMM2 suggested that the responses to stranger scat were stronger than to neighbor scats. Stranger scats were investigated for a significantly longer duration by the dominant pair than other pack members (stranger: 9.20; 95% CI $= 4.76$–13.65; $p < 0.001$) (Fig. 4, Table 4). We also found that the intensity of response to strangers increased as the resident dhole pack size increased (0.83; 95% CI $= 0.38$–1.28; $p < 0.001$) (Fig. 5, Table 5). Furthermore, dholes investigated stranger scats for a significantly longer duration irrespective of the location (core or buffer) of the recipient pack's territory (2.55; 95% CI $= 0.38$–1.28; $p < 0.01$) (Fig. 6, Supplementary 5).

Overall, results indicate that dholes investigated scats from strangers for longer than they did scats from neighbors, irrespective of where are these scats were encountered in their territory. This provides support for the dear enemy phenomenon in dholes.

Discussion

Territoriality and inter-pack dynamics have not been systematically explored in the wild for cryptic species like the dholes. From our study, we demonstrated that dholes

Table 2 List of models and their details examining the differences in the response to controls (soil and own) vs treatments (neighbor and stranger) in scat translocation experiments on dholes in TATR.

Model averaging was done for the two models with ΔAIC values < 2 to arrive at the top model

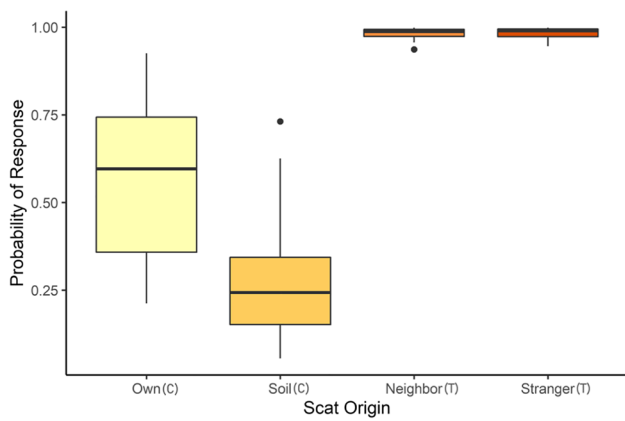| Models	Variables	df	logLik	AIC	Delta	Weight
1	~ pack.size + responder + scat.origin + (1 | pack)	8	−43.6	104.06	0	0.55
2	~ pack.size + scat.origin + 1| pack)	6	−46.51	105.51	1.45	0.27
3	~ core.buffer + pack.size + responder + scat.origin + (1 | pack)	9	−43.58	106.23	2.17	0.19

Fig. 3 Predicted probability of response of dholes to different donor groups (controls—soil and own; treatments—neighbor and stranger) in the scat translocation experiments, Tadoba Andhari Tiger Reserve, India. Controls are marked C and treatments are marked T from the model output of the top model. Box plot showing median (bold line), quartile (50% of data within the box), and the maximum and minimum value (edge of whiskers) excluding outliers (black circles), i.e., the points falling out of the 25–75 percentile range

investigate and counter-mark stranger scent marks more intensively than those of neighboring/familiar packs, thereby exhibiting the dear enemy hypothesis.

Dear enemy or nasty neighbor

Overall, unfamiliar/stranger packs elicited more intensive responses than neighbors across the core and buffer areas of the packs. Consistent with results from studies on a range of species (including birds, e.g., Krebs 1982; Jin et al. 2021; mammals, e.g., Barash 1974; Vázquez et al. 2020; reptiles, e.g., Fox and Baird 1992; Quintana and Galdino 2017; amphibians, e.g., Jaeger 1981; Tumulty and Bee 2021; fish, e.g., Peeke et al. 1971; Sogawa and Kohda 2018; insects, e.g., Heinze et al. 1996; Trigos-Peral et al. 2021; crabs,

Table 3 Summary of the averaged model from scat translocation experiments of dholes in Tadoba Andhari Tiger Reserve, India

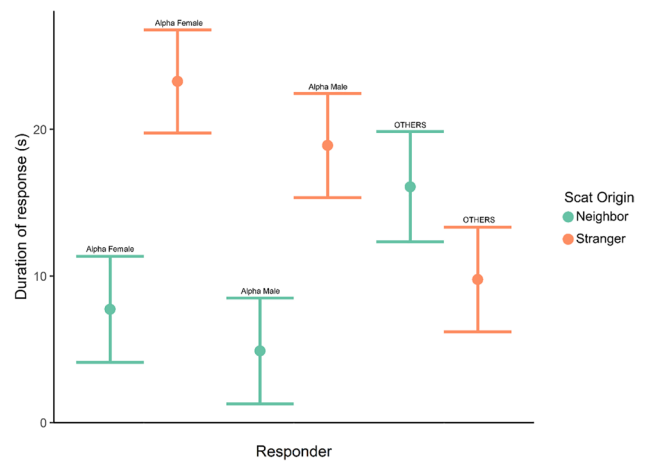| Predictors	Log-Odds		CI
Intercept (alpha female; neighbor)	5.93	***	3.30–8.57
Pack size	−0.23	**	−0.40 to −0.06
Alpha male	−0.39		−1.63 to −0.85
Others	1.26		−0.18–2.69
Own	−3.94	***	−6.11 to −1.78
Soil	−5.46	***	−7.82 to −3.11
Stranger	0.16		−2.68–2.99
N pack	4		
Observations	177		

*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$

Fig. 4 Predicted intensity of response for interactions between scat origin groups (neighbors vs. strangers) and responder groups (alpha male; alpha female; and other pack members) from scat translocation experiments on dholes, Tadoba Andhari Tiger Reserve, India, from the model output of the top model. Points denote mean predicted intensity values, while bars represent upper and lower 95% confidence intervals

Table 4 Summary of the fixed effect estimates from the best fit GLMM from scat-translocation experiments of dholes in Tadoba Andhari Tiger Reserve, India

Predictors	Estimates		CI
Intercept (alpha female; neighbor; buffer)	10.02	***	4.32–15.72
Pack size	−0.35		−1.02–0.32
Core	−1.17		−3.32–0.98
Alpha male	−2.84	*	−5.38 to −0.30
Others	8.36	***	5.73–10.99
Stranger	9.20	***	4.76–13.65
Core × stranger	2.55	*	−0.43–5.52
Alpha male × stranger	−1.53		−5.08 to −2.02
Others × stranger	−21.87	***	−25.50 to −18.24
Pack size × stranger	0.83	***	0.38–1.28
Random effects			
σ^2	15.96		
$\tau_{00\ pack}$	4.35		
ICC	0.21		
N_{pack}	4		
Observations	115		
R^2	0.77		

*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$

e.g., Fogo et al. 2019), our study revealed compelling evidence that dholes exhibit the dear enemy phenomenon in which animals reduce the costs associated with territorial defense. However, group-living species may exhibit behavioral plasticity that can be adapted according to the social
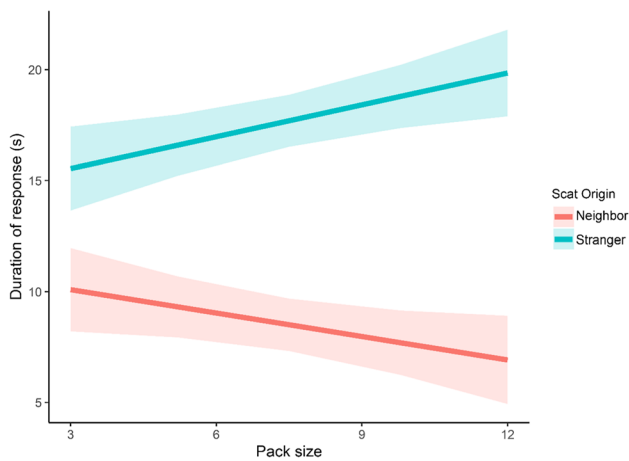
Fig. 5 Predicted intensity of response for interactions between scat origin groups (neighbors vs. strangers) as pack size increases from scat translocation experiments on dholes, Tadoba Andhari Tiger Reserve, India, from the model output of the top model. Lines denote the mean predicted intensity values, while ribbons (shaded areas) represent 95% confidence intervals

environment of the species. Several authors have discussed that defensive responses to territorial intruders may depend on multiple factors like population densities, group sizes of the interacting packs, seasonal changes in the social context, frequency of intrusions, and degree of aggressiveness of different neighbors (Temeles 1994; Radford 2008; Müller and Manser 2007; Mitani et al. 2010; Bee et al. 2016; Christensen and Radford 2018; Tumulty and Bee 2021).

Furthermore, we observed a within species—within group variation in the response to intruders. Dholes are obligate cooperative breeders in that one pair monopolizes the breeding rights—the alpha male and the alpha female, whereas the non-breeding pack members aid in raising the offspring of the alpha pair. The intensity of behavioral responses differed depending upon the dominance status of

pack members. Individual members of groups have been studied to differ in their responses to the same territorial intrusion (Beehner and Kitchen 2007; Christensen and Radford 2018). The scats of the neighbors were investigated intensively by the non-dominant adults or the sub-adults from the packs, whereas the breeding pair responded more strongly to the stranger group scent marks. The dominant pair would not spend their energy to inspect neighbor scent marks as intensively as strangers based on their familiarity. This pattern could also be a function of kin-clustering resulting from natal philopatry where the dispersing individuals establish themselves in close proximity of their natal ranges as observed in African wild dogs (Jackson et al. 2017). Moreover, the pack leaders may have to be more alert and proactive in territorial defense against unfamiliar packs as they have more to lose than sub-ordinate members in terms of mating success (Beehner and Kitchen 2007). Previous studies on pack living species like coyotes and wolves have shown that the alpha members of a pack were principally responsible for maintaining and defending the territory thereby playing a more critical role in territorial defense (Mech 1970; Peters and Mech 1975; Gese 2001). Further experiments are warranted to determine if subdominant animals react less intensively to stranger scent information as a strategy that may assist their dispersal across a landscape where intraspecific conflict is likely. Additionally, the fine-scale differential behavioral response between the responder groups could also be due to the different information that the olfactory cues communicate to the recipients. The alpha females were reported to investigate the scent marks of strangers more intensively than the alpha males. One explanation for this observation could be the sex-biased dispersal in dholes wherein the females disperse to join other packs or form a new pack (S. Modi et al. unpublished data). Hence, the intensive examination of scats could be to obtain information of the donor pack and not merely a form of

Table 5 List of competing models and their details examining the differences in the intensity of response to controls vs treatments in scat translocation experiments on dholes in TATR

Model selection table

| Models	Variables	df	logLik	AICc	AIC	delta	weight
Mod1	~ pack.size + core.buffer + responder + scat.origin + scat.origin X core.buffer + scat.origin X responder + scat.origin X pack.size + core.buffer X scat.origin + (1 | pack)	12	−326.77	680.6		0.00	0.72
Mod2	~ pack.size + core.buffer + responder + scat.origin + scat.origin X core.buffer + scat.origin X responder + scat.origin X pack.size + core.buffer X pack.size + core.buffer X scat.origin + (1 | pack)	13	−326.52	682.65		2.05	0.26
Mod3	~ pack.size + core.buffer + responder + scat.origin + scat.origin X core.buffer + scat.origin X responder + scat.origin X pack.size + core.buffer X responder + core.buffer X pack.size + core.buffer X scat.origin + (1 | pack)	15	−326.34	687.53		6.93	0.02

Models ranked by AIC(x)
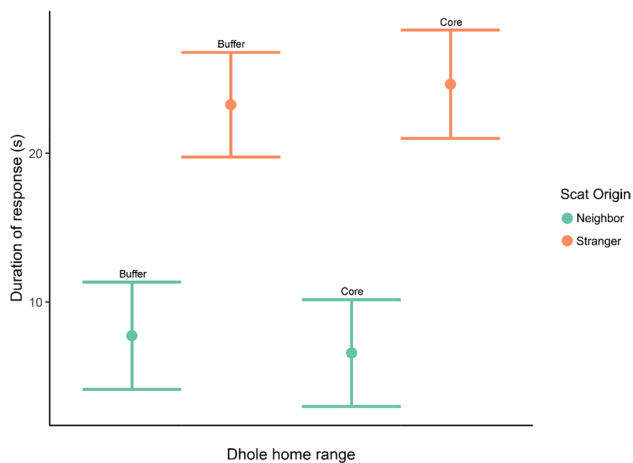
Fig. 6 Predicted intensity of response for interactions between scat origin groups (neighbors vs. strangers) in core (C) vs. buffer (B) of dhole packs from scat translocation experiments on dholes, Tadoba Andhari Tiger Reserve, India, from the model output of the top model. Points denote mean predicted intensity values, while bars represent upper and lower 95% confidence intervals

territorial defense in the case of the alpha females. To summarize, interactions like the dear enemy or nasty neighbor phenomena seem context dependent and flexible rather than a fixed behavioral pattern (Monclús et al. 2014). Further studies using molecular tools would aid in understanding the intricacies of social interactions in dholes. Our results also suggested that irrespective of the location of the scats of conspecifics within the home range of a resident pack, the stranger scats were investigated for a significantly longer duration than neighbors. This suggests that the neighbors were considered less of a threat than unfamiliar conspecifics. Thus, the dear enemy phenomenon in dholes is most likely an evolutionary response to the high cost and low payoff of escalated aggression between territorial neighbors.

Effect of dhole pack size on response

Our results indicated that overall, the probability of response to scat translocation experiments by resident packs significantly decreased as the pack size increased (Supplementary 4). This could be a function of reduced territorial aggression as larger groups are known to dominate the smaller groups in inter-group encounters (Harrington and Mech 1979; McComb et al. 1994; Cheney 2008; Creel and Creel 2015; Jackson et al. 2017) (but see Crofoot et al. 2008; Jordan et al. 2017). On a finer scale, we also found that the intensity of response to neighboring packs decreased with an increase in resident packs size, whereas it increased for stranger packs (Fig. 5). This could mean that in larger packs, neighbors are considered less of a threat than strangers or that it simply takes less time to decipher the relevant information from

familiar (neighbor) scats than strangers. Studies have shown that numerical assessment is widespread among species with intergroup contests (McComb et al. 1994; Wilson et al. 2001; Furrer et al. 2011).

The importance of scent marking in territory defense could be overemphasized, and other functions such as reproductive competition may be an important driving force behind these behavioral patterns (Jordan et al. 2010). This may not be the case for the breeding pair that reacts strongly to strangers, but other pack members from larger groups may be looking for dispersal/mating opportunities. Further experiments with more variation in resident pack sizes and variation in number of presented scats would aid in understanding this relationship better.

A note on counter-marking

On evaluating the types of response to the stimuli presented, our results showed that the most common response to any treatment was "inspection bout + counter-marking" or "over-marking" (Fig. 2). Of the 35 experiments without a response from dhole packs, 94.29% ($n = 33$), were controls suggesting that the dholes almost always responded to conspecific scents (Supplementary 1). Counter-marking primarily at the treatment sites may suggest that this type of response has a role in communication olfactory cues with conspecifics.

Growing evidence suggests over-marking of scent marks is universal in terrestrial mammals (Johnson 1973; Mac-Donald 1980; Sillero-Zubiri and MacDonald 1998; Sliwa and Richardson 1998; Brashares and Arcese 1999; Lewis 2005). It has even been described as a specialized form of olfactory communication that is demonstrably disparate from typical scent marking (Ferkin and Pierce 2007). Moreover, various hypotheses have been put forth, not mutually exclusive of each other, on the function of scent over-marking in multiple species. Over-marking in dholes may have multiple functions as well. Dholes may over-mark or "counter-mark" the scent of a conspecific as competition to be the top-most scent donor, suggesting a higher social rank (Rich and Hurst 1998; Ferkin and Pierce 2007) or posing a threat (Smith and Abbott 1998; Ferkin and Pierce 2007). Over-marking may also serve as a "bulletin board" to communicate inter- and intra-pack using olfactory cues, a form of self-advertisement, mate guarding, a form of mate attraction, a guide for navigation, and the formation of a group/colony scent. Such behavior has been extensively documented in hyenas *Crocuta crocuts* (Drea et al. 2002), gray wolves (Sillero-Zubiri and Macdonald 1998), aardwolves *Proteles cristatus* (Sliwa and Richardson 1998), marmots *Marmota marmota* (Bel et al. 1999), antelopes *Oreotragus oreotragus* (Roberts and Dunbar 2000), beavers *Castor fiber* (Rosell and Bergan 2000), ring-tailed lemurs *Lemur catta* (Hayes et al. 2004), tamarins

Saginus mystax, gerbils *Meriones unguiculatus*, voles *Microtus* spp., ratel (Ferkin and Pierce 2007), and African wild dogs (Jordan et al. 2014). We would like to highlight that on multiple occasions ($n = 17$), the breeding females were observed to do a hand-stand and mark the same spot as the breeding male by balancing on the forelegs, finally over-marked by the males (Ghaskadbi et al. 2016). Such a counter-marking ritual of the breeding pairs has also been observed in wolves (Rothman and Mech 1979), golden jackals *Canis aureus* (Golani and Mendelssohn 1971), crab-eating foxes *Cerdocyon thous* (Brady 1979), and bat-eared foxes *Otocyon megalotis* (Lamprecht 1979), and is believed to synchronize reproductive states and inform conspecifics of the pair's bond (Rothman and Mech 1979). On some occasions, male dholes were also observed performing handstand urination events ($n = 9$) to deposit the top-most scent. Studies have reported similar behavioral patterns in species like dwarf mongooses *Helogale parvula* (Rasa 1973), bush dogs *Speothos vanaticus* (Porton 1983), giant pandas *Ailuropoda melanoleuca* (White et al. 2002), and African wild dogs (Jordan et al. 2014). In the past, several studies on canids have shown that the rate of scent marking is higher in the breeding pair than in non-breeding individuals (Sillero-Zubiri and Macdonald 1998; Gese and Ruff 1997; Zub et al. 2003; Tshimologo 2014). Nevertheless, overall, we observed both breeding and non-breeding members of the packs' scent marking, which supports both territorial defense and mate guarding strategies and highlights its importance as a form of communication with conspecifics.☐☐☐☐☐☐☐☐☐☐☐☐☐☐

Conclusion

Our experiments elucidate that dholes used scent marks as a form of territorial maintenance and exhibited neighbor-stranger discrimination. Overall, they exhibited the dear enemy phenomenon with an increased response to scent marks of stranger packs, whereas the response was less intensive for familiar, established neighbors. The dominant pair were observed to respond more intensively than other pack members to strangers suggesting that the response may not be fixed but context dependent. The stranger packs were considered a threat irrespective of the location they were encountered in a resident pack's territory. Long-term, multi-disciplinary studies on the role of olfactory communication in territorial maintenance and defense in dholes would enhance our understanding of the biology of a rare and endangered species. Similar findings from studies on territorial behavior have been applied to actively manage another closely related, endangered species—the African wild dogs (Jackson et al. 2012). Scent marks act as biological barriers that facilitate the shaping and limiting of territories, and

translocated African wild dogs were supported in establishing new territories with an understanding of their territorial behavior (Jackson et al. 2012; Ausband et al. 2013). We suggest that the conservation of endangered carnivores in India could greatly benefit from applied behavioral research that has immense potential in terms of management implications.

Author contribution All authors (P. G., P. N., B. H.) contributed to the study conception and design. Material preparation, data collection, and analysis were performed by P. G. The first draft of the manuscript was written by P. G. and all authors (P. G., P. N., B. H.) commented on all versions of the manuscript. All authors read and approved the final manuscript.

Availability of data and material All data generated or analyzed during this study are included in this published article [and its supplementary information files].

Code availability The R Code has been attached as a supplementary file.

Declarations

Ethics approval The authors obtained a Dhole capture permit (MFD-SPP-12/05.11.2016) for the radio-collared dholes in the study. All applicable international, national, and/or institutional guidelines for the use of animals were followed.

Consent for publication All authors have given consent for submission of the manuscript.

Conflict of interest The authors declare no competing interests.

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