Olfactory communication to protect livestock: dingo response to urine marks of livestock guardian dogs

Linda van Bommel[A,B,C] *and Chris N. Johnson*[A]

[A]School of Biological Sciences, University of Tasmania, Private Bag 55, Hobart, Tas 7001, Australia.
[B]Fenner School of Environment and Society, Australian National University, Canberra, ACT 2601, Australia.
[C]Corresponding author. Email: linda.vanbommel@anu.edu.au

Abstract.   The behavioural mechanisms by which livestock guardian dogs (LGDs) protect livestock from wild predators are not yet fully understood. LGD urine could play a part, as scent-marking the boundaries of a territory could signal occupation of the area to predators. Past selection for dogs that were most effective in deterring predators could have resulted in LGDs that produce urine with predator-deterrent properties. In this research, 28 captive dingoes (14 male and 14 female) were tested for their response to urine marks of LGDs (Maremma sheepdogs), herding dogs (Border Collies) and other dingoes, with distilled water used as a control. The response of the dingoes to the scents was measured using eight variables. For most variables, the response to the test scents was not statistically different from the response to the control. Test *minus* control was calculated for each test scent category, and used to compare responses between different test scents. The response to Maremma urine was similar to the response to Border Collie urine, and resembled a reaction to a conspecific. We found no evidence of predator-repellent properties of LGD urine. Our results suggest that dingoes readily engage in olfactory communication with Maremmas. It therefore seems likely that they would recognise territorial boundaries created by working Maremmas.

Additional keywords: deterrent, LGD, LPD, scent marking, territoriality.

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Introduction

In Australia, predators cause substantial losses to the livestock industry (Gong *et al*. 2009; Fleming *et al*. 2014). Wild dogs, including dingoes (*Canis dingo*), feral dogs (*Canis familiaris*) and their hybrids, are the most significant predators, as they prey on most livestock species over the entire continent, while smaller predators target smaller stock. The greatest damage is caused to the sheep and cattle industries (Gong *et al*. 2009; Fleming *et al*. 2014). Lethal control of predators is often used to protect livestock (Fleming *et al*. 2014); however, various non-lethal methods are also available (van Bommel and Johnson 2014*a*).

Livestock guardian dogs (LGDs) (*Canis familiaris*) have a long history of protecting livestock from predators and thieves in Europe and Asia (Coppinger and Coppinger 2001). These are generally dogs of large breeds that live with livestock fulltime, and they can be effective in protecting a range of livestock species from several types of predators, both on small properties and extensive livestock operations (older studies reviewed in Rigg 2001; see also Hansen *et al*. 2002; Marker *et al*. 2005; Otstavel *et al*. 2009; Gehring *et al*. 2010; Rigg *et al*. 2011; van Bommel and Johnson 2012). In Australia, LGDs are relatively uncommon, but they are increasing in popularity (van Bommel and Johnson 2012). The Maremma Sheepdog (Maremma) is the LGD breed that is most readily available, and

is therefore the breed of choice for most Australian farmers looking for a LGD (van Bommel and Johnson 2012).

While the presence of LGDs can reduce predation on livestock, it is not fully understood how LGDs accomplish this task. LGDs could provide direct protection to livestock by reacting to predators that closely approach their stock. This reaction could consist of aggressively confronting and driving off predators (McGrew and Blakesley 1982; Lorenz and Coppinger 1986). In addition, territorial behaviour could also be an important component of livestock protection (van Bommel and Johnson 2014*c*). Avoidance by predators of areas occupied by LGDs would reduce predator activity around stock. In addition, predators that enter these areas might reduce their hunting in response to the risk of detection by LGDs. Maremmas have been found to enforce territorial boundaries (van Bommel and Johnson 2014*c*), and territorial behaviours such as scent marking, regular barking and boundary patrolling have been observed in LGDs in several studies (Linhart *et al*. 1979; McGrew and Blakesley 1982; Green and Woodruff 1983; Black and Green 1985; Hansen and Bakken 1999; van Bommel and Johnson 2014*b*, 2014*c*).

Scent marking by canids and other mammalian predators is an important aspect of territorial behaviour (Peters and Mech 1975; Gese and Ruff 1997; Sillero-Zubiri and Macdonald 1998). Possible roles of scent marking include delineation of territorial

boundaries (Peters and Mech 1975; Allen *et al*. 1999), and informing conspecifics of the sex, reproductive status, body size and condition of the marker (Rothman and Mech 1979; Gese and Ruff 1997). It has also been hypothesised that scent marks can inform competing predators of the marker's presence (Paquet 1991; Scheinin *et al*. 2006). Furthermore, predator scent marks can be a deterrent for prey species (Epple *et al*. 1993; Woolhouse and Morgan 1995; Parsons *et al*. 2007). It is currently unknown what role olfactory communication plays in livestock protection by LGDs. Scent marks from LGDs could signal territorial occupation to other predators. Most LGD breeds have been selected for centuries for the specific task of livestock protection (Coppinger and Coppinger 2001). This could have led to selection for LGDs that produce scent marks that not only signal occupation of territory, but also have predator-deterrent properties, similar to the deterrent effect that predator scent marks can have on their prey species (Apfelbach *et al*. 2005; Parsons and Blumstein 2010*a*, 2010*b*).

In this study, we investigated whether urine marks from LGDs have predator-deterrent properties. Dingoes were presented with the urine of Maremmas, Border Collies (*Canis familiaris*) and other familiar dingoes. Border Collie urine was included in the experiment to compare the effect of the urine of a LGD to that of a non-LGD domestic dog. While both LGDs and herding dogs, such as Border Collies, work with livestock, their function is very different (Coppinger and Coppinger 2001). Border Collies are unsuitable as LGDs as they lack the proper character attributes for this function, due to a long period of selection for specific herding traits (Coppinger and Coppinger 2001). Border Collies are therefore unlikely to have developed predator-deterrent properties in their urine, as they have not undergone the same selection process for livestock guardian traits as LGDs. Border Collies are often found on farming properties and dingoes could therefore regularly encounter their urine marks.

The urine of dingoes was included to compare the effect of the urine of Maremmas and Border Collies to the effect of urine from other dingoes. Our hypothesis was that if the Maremma urine has evolved to contain predator-deterrent properties, similar to the deterrent effect some predator urine can have on their prey species, the dingoes would quickly locate it, investigate it, move away from the scent, and actively avoid it from then on. Alternatively, if the Maremma urine does not have predator-deterrent properties, we would expect the dingoes to respond to the urine from the Maremmas in a similar manner as to the urine from the Border Collies. We expected the dingoes to quickly locate the Border Collie urine, investigate it, and leave marks in return, as it would represent a urine mark from an unfamiliar canid. As the dingoes were familiar with the urine of the dingoes used in this experiment, we expected them to take longer to locate the urine, and spend less time investigating it, as the odours are already familiar and do not require further investigation.

Methods

Research facility

The dingoes were all housed at the Dingo Discovery and Research Centre, near Gisborne, Victoria, as male–female pairs in kennels measuring 30 m^2. Each pair got daily exercise in one of five large outdoor enclosures measuring between 100 and 250 m^2. The animals were fed once a day with a mixture of fresh meat and commercial dry dog food. In all, 28 dingoes were used in this research, 14 males and 14 females. All animals were sexually intact, and had been DNA tested and confirmed as pure dingo (using the method described in Wilton 2001). The experiment was done in July 2012, and took four days to complete. Most dingo pairs had pups ranging in age from two to six weeks at the time of the research.

Experimental setup

Dingoes were tested in pairs. Each pair was tested for their response to (1) Maremma urine, (2) Border Collie urine and (3) dingo urine. Distilled water was used as a control. Only urine from mature, sexually intact males was used in the experiment. The urine was collected in the two weeks leading up to the experiment, and stored in glass bottles in a fridge after collection until it was used. Urine was obtained from three different Border Collie males, and from each of four different Maremma and dingo males. Urine from individual males was stored in separate glass bottles. Border Collie urine was collected from dogs owned by a dog trainer near Braidwood, New South Wales, Maremma urine was collected from dogs owned by a Maremma breeder near Shepparton, Victoria, and dingo urine was collected from dingoes held at the Dingo Discovery and Research Centre. Care was taken that individual dingoes were not presented with their own urine as a test.

Dingo pairs were tested in one of the outside enclosures during their daily exercise time. Each pair was tested only once a day. The three categories of urine were presented to them on three consecutive days, always in the same outside enclosure for each pair. Distilled water was used as a control on each day. The dingoes were left a minimum of 45 min in the enclosure for the test. Two steel star pickets were used to present the urine and the distilled water to the dingoes. Each picket was marked with 1–2 mL of either urine or water, and set up before the dingoes were allowed into the enclosure. The marks were applied ~15 cm above ground level. The pickets were at least 1 m apart. The location of the pickets was changed at the end of each test; locations were selected away from naturally occurring vegetation or vertical objects that would present convenient scent-marking spots in each dingo's normal day-to-day olfactory communications. Human scent left in the outside enclosures was not considered a problem, as people regularly entered the enclosures for cleaning or to interact with the dingoes. Pickets were removed after each experiment, and thoroughly cleaned between experiments by hosing them down, and then liberally spraying them twice with an enzyme solution that biologically breaks down scent molecules (Nature's Miracle Scentless Odor Destroyer, Nature's Miracle, OH, USA). All pickets also underwent this treatment before their first use in the experiment. The pickets were allowed to dry naturally between cleaning treatments. In addition, the ground immediately around the location where the pickets had been set up in each experiment was also sprayed liberally with the same enzyme solution, in an attempt to remove traces of the scent of urine that might have fallen on the ground. The scent of any scent marks that were left by the dingoes themselves in response to the experiment was not considered a problem, as the dingoes freely

engaged in olfactory communication with each other on a day-to-day basis in the outdoor enclosures as part of their normal activities. The experiment was randomised in a balanced design with regard to (1) the order in which the three categories of test urine were presented to each dingo pair, (2) the identity of the male from which the urine had been obtained, and (3) which picket was marked with the test urine versus distilled water.

Digital video recorders were used to record the dingoes' behaviour during each test; one recorder was aimed at each picket, and the two recorders could observe the dingoes' behaviour almost anywhere in the enclosure most of the time. Digital voice recorders were used to record any vocalisations that were made by the dingoes during the experiment. Direct observation of the experiments was not possible.

Data analysis

To standardise the time over which the analysis was done, 30 min of recordings were used for each dingo pair for each test, starting from the moment the pair entered the enclosure. One researcher analysed all the video recordings, and measured the following variables: (1) whether a picket was sniffed or not, (2) if sniffed, latency to sniff (s); (3) total number of times that the picket was sniffed; (4) average time per sniff (s); (5) whether a picket was scent marked or not; (6) number of scent marks aimed at the picket, or within 1 m of the picket if clearly in response to the test urine or the distilled water on the picket; (7) type of mark used; and (8) number and type of vocalisations in response to the test urine or the distilled water. The male and female of each pair were easily distinguishable from each other,

and these variables were measured for the male and the female of the pair separately. In general, males had a higher response than females (Table 1). Males and females might have different motivations for behaviour in response to urine from other male dogs; therefore, the data from males and females were analysed separately.

Data analysis was exploratory, aimed at finding any strong effects that might have been present in the data. Variable 7 is described only, as sample sizes were too small for valid statistical analysis. Variable 8 could not be analysed, as no vocalisations were recorded during the trials. To test for differences in response variables between test urine (dingo, Border Collie or Maremma) versus control (distilled water), paired *t*-tests were used for Variables 2, 3, 4 and 6, and McNemar's test was used for Variables 1 and 5.

Differences in response to the different categories of test urine

The difference in response between test and control was calculated (test *minus* control) for each response variable for each individual. Then, for each response variable, these new values were entered in a general linear mixed model as the dependent variable. Dog identity and trial number (1–3, for the three days in which each of the categories of urine were presented to each pair) were entered as random variables, to account for individual variation in response and to account for the influence of trial number. For each response variable, two models were created: (1) with urine category as an explanatory variable, and (2) including only the random variables. These two

Table 1. Mean responses for the variables measuring responses of male and female dingoes to the three test scents
All variables are summarised as means ± s.e.

Variable	Male		Female	
	Test scent	Control	Test scent	Control
1. Picket found or not				
Maremma	0.79 ± 0.11	0.64 ± 0.13	0.57 ± 0.14	0.64 ± 0.14
Dingo	0.71 ± 0.13	0.79 ± 0.11	0.79 ± 0.11	0.64 ± 0.13
Border Collie	1.00 ± 0.00	0.57 ± 0.14	0.86 ± 0.10	0.50 ± 0.14
2. Time until picket was found (s)				
Maremma	310.14 ± 81.19	366.00 ± 134.30	624.33 ± 228.94	368.67 ± 110.25
Dingo	422.30 ± 118.54	314.7 ± 90.77	319.13 ± 111.76	477.63 ± 143.97
Border Collie	182.25 ± 111.01	400.75 ± 113.49	482.33 ± 176.66	470.11 ± 171.16
3. Total number of sniffs				
Maremma	2.57 ± 0.68	1.71 ± 0.64	1.00 ± 0.28	0.86 ± 0.25
Dingo	1.22 ± 0.33	1.22 ± 0.49	1.14 ± 0.23	0.86 ± 0.25
Border Collie	2.36 ± 0.37	1.50 ± 0.48	1.64 ± 0.34	0.71 ± 0.24
4. Average time per sniff (s)				
Maremma	7.76 ± 0.98	1.56 ± 0.45	3.55 ± 1.32	1.49 ± 0.50
Dingo	3.63 ± 1.13	2.19 ± 0.61	2.62 ± 1.11	2.99 ± 1.14
Border Collie	8.84 ± 1.44	1.70 ± 0.58	8.38 ± 1.52	1.79 ± 0.66
5. Picket scent-marked or not				
Maremma	0.50 ± 0.14	0.14 ± 0.10	0.00 ± 0.00	0.00 ± 0.00
Dingo	0.21 ± 0.11	0.36 ± 0.13	0.14 ± 0.10	0.21 ± 0.11
Border Collie	0.29 ± 0.13	0.07 ± 0.07	0.07 ± 0.07	0.00 ± 0.00
6. Number of scent-marks				
Maremma	1.07 ± 0.43	0.64 ± 0.44	0.00 ± 0.00	0.00 ± 0.00
Dingo	0.93 ± 0.43	0.50 ± 0.25	0.29 ± 0.16	0.14 ± 0.10
Border Collie	0.71 ± 0.35	0.21 ± 0.21	0.07 ± 0.07	0.00 ± 0.00

models were ranked according to their AICc weight (Symonds and Moussalli 2011), and the strength of the evidence for an effect of the category of urine on the response variable was assessed.

Influence of identity of the male from which the urine was obtained

To investigate whether dingoes consistently responded differently to urine marks of individuals within each test urine category, for each response variable the individual males within each category (Maremma, Border Collie, dingo) were ranked according to the strength of the response that their urine elicited in the dingoes (1 for the male that elicited the strongest response, 2 for second strongest, etc). The difference between test and control (see previous section) was used to assess the strength of response; the strongest response was defined as the greatest difference between test and control for Variables 1, 3, 4, 5 and 6, and the smallest difference for Variable 2. Within each test urine category, the rankings of the individual males for each of the six response variables were tested for differences in overall rank using a Friedman test.

All analyses were done with R statistical software (R Development Core Team 2008). General linear mixed models were analysed in R using the package 'lme4' (Bates *et al.* 2014).

Results

Test (urine of dingo, Border Collie or Maremma) versus control (distilled water)

Male and female dingoes generally did not respond to the urine of another dingo in a way that was significantly different from distilled water, with the exception of the variable 'total number of sniffs'. For this variable male dingoes sniffed distilled water significantly more often than the dingo urine ($t = -2.4$, d.f. $= 13$, $P < 0.03$). No significant differences were found in female dingoes' response to Maremma urine compared with distilled water for any of the variables, but for male dingoes the response to Maremma urine was significantly higher than for distilled water for one variable: 'average time per sniff' ($t = 3.0$, d.f. $= 12$, $P < 0.01$). Female dingoes had a significantly higher response to Border Collie urine compared with distilled water for two variables: 'total number of times the picket is sniffed' ($t = 2.6$, d.f. $= 13$, $P < 0.05$) and 'average time per sniff' ($t = 5.0$, d.f. $= 13$, $P < 0.01$). Males also had a significantly higher response to Border Collie urine compared with distilled water for two variables: 'whether the picket was sniffed or not' (exact McNemar, $P < 0.05$) and 'average time per sniff' ($t = 4.3$, d.f. $= 13$, $P < 0.01$).

Comparison between the categories of test urine

For male dingoes, the urine of Maremmas and Border Collies elicited a higher response than the urine of dingoes for all variables (Table 1). The Variables 2 ('latency to sniff'), 3 ('number of sniffs'), 4 ('average time per sniff') and 6 ('number of scent marks') were all influenced by the category of urine in the experiment (Table 2); for these variables, the model including urine category as an explanatory variable ranked as a better fit to the data than the model with only the random variables. For two of these variables – 3 ('number of sniffs') and 6 ('number

of scent marks') – the response to Maremma urine was higher than to Border Collie urine, whereas for the other two variables – 2 ('latency to sniff') and 4 ('average time per sniff') – it was the opposite (Table 1).

For female dingoes, the response to dingo urine was highest for three variables: 1 ('picket sniffed or not'), 2 ('latency to sniff'), and 3 ('total number of sniffs') (Table 1). For Variables 4 ('average time per sniff') and 5 ('picket scent marked or not') the response was highest for Border Collie urine, and for Variable 6 ('number of scent marks') was highest for Maremma urine (Table 1). Variables 2 ('latency to sniff'), and 4 ('average time per sniff') were influenced by the urine category in the experiment; for these variables the model including urine category fit the data better than the model that included only the random variables (Table 2).

For the other two variables for males and four variables for females the model that included urine category as an explanatory variable did not fit the data better (and it was sometimes worse) than the model with only the random variables (Table 2).

Types of scent marks used

The main type of scent mark used by both males and females was standing raised-leg urination (RLU), which in approximately half of the cases was followed by ground scratching (GS) (Table 3). Defaecation was used as a scent mark by only one male, in response to Maremma urine and dingo urine (Table 3).

Identity of the individuals from which the urine was obtained

See Table 4 for the mean ranking of the individual males from which the urine was obtained. The rank of individual Maremmas, based on the dingoes' strength of response to their urine marks, was consistently different between the six response variables for male dingoes ($\chi^2_3 = 11.28$, $P = 0.01$), but not for females ($\chi^2_3 = 6.39$, $P = 0.09$). This ranking for Border Collies was consistently different between the six response variables for female dingoes ($\chi^2_2 = 8.32$, $P = 0.02$), but not for males ($\chi^2_2 = 2.70$, $P = 0.26$). Similarly, for dingoes, this ranking was also consistently different between the response variables for females ($\chi^2_3 = 11.59$, $P = 0.03$), but not for males ($\chi^2_3 = 4.07$, $P = 0.25$).

Discussion

No avoidance of Maremma urine marks was observed during this experiment, nor did we record any other behaviour indicating that the test dingoes were deterred by the Maremma marks. On the contrary, Maremma marks were actively investigated, and elicited a similar response in the test dingoes to Border Collie marks. This indicates that Maremma urine does not have any deterrent properties for dingoes. The response to Maremma and Border Collie marks more closely resembles olfactory communication with a conspecific: the urine is acknowledged, investigated and a scent mark is often left in response (Sillero-Zubiri and Macdonald 1998).

The high response to the distilled water, which meant that there were relatively few statistically significant differences between test and control for most variables, is probably caused by two factors. First, the dingoes were unfamiliar with the star

Table 2.   Outcomes of the generalised linear mixed models

Individual- and trial number were always used as random variables. In the 'scent' model, the type of scent was used as an explanatory variable; in the 'only random variables' model, the model included only the random variables

	Model	AICc	ΔAIC	AIC weight	Relative likelihood
Males					
1. Picket sniffed or not	1. Only random variables	72.14	0.00	0.5	1.0
	2. Scent	72.62	0.48	0.5	1.0
2. Latency to sniff	1. Scent	627.22	0.00	1.0	1.0
	2. Only random variables	657.99	30.77	0.0	0.0
3. Total number of sniffs	1. Scent	188.26	0.00	0.9	1.0
	2. Only random variables	193.34	5.08	0.1	0.0
4. Average time per sniff	1. Scent	444.74	0.00	1.0	1.0
	2. Only random variables	463.25	18.51	0.0	0.0
5. Picket scent-marked or not	1. Only random variables	76.78	0.00	0.7	1.0
	2. Scent	78.92	2.14	0.3	0.4
6. Number of scent-marks	1. Scent	157.83	0.00	1.0	0.8
	2. Only random variables	160.38	2.57	0.0	0.2
Females					
1. Picket sniffed or not	1. Only random variables	84.32	0.00	0.5	1.0
	2. Scent	84.82	0.50	0.5	1.0
2. Latency to sniff	1. Scent	268.06	0.00	1.0	1.0
	2. Only random variables	292.36	24.30	0.0	0.0
3. Total number of sniffs	1. Only random variables	146.81	0.00	0.7	1.0
	2. Scent	148.81	2.00	0.3	0.0
4. Average time per sniff	1. Scent	418.34	0.00	1.0	1.0
	2. Random variables	443.66	25.32	0.0	0.0
5. Picket scent-marked or not	1. Only random variables	6.00	0.00	1.0	0.0
	2. Scent	13.98	7.98	0.0	1.0
6. Number of scent-marks	1. Only random variables	21.91	0.00	0.9	1.0
	2. Scent	27.37	5.46	0.0	0.0

Table 3.   The number of times the dingoes used different types of scent-mark postures

RLU, standing raised leg urination; GS, ground scratching

		Male		Female	
		Test scent	Control	Test scent	Control
Maremma	RLU with GS	10	6	0	0
	RLU	4	3	0	0
	Defaecation	1	0	0	0
Dingo	RLU with GS	0	6	2	1
	RLU	4	9	1	2
	Defaecation	1	0	0	0
Border Collie	RLU with GS	5	1	0	0
	RLU	5	3	1	0
	Defaecation	0	0	0	0

Table 4.   Mean ranking over the six response variables of individual males within each scent category, based in the strength of the response elicited by their urine in the dingoes

	Males		Females	
Maremma	Tebaldo	1.3 ± 0.2	Solhario	1.6 ± 0.2
	Llianno	1.8 ± 0.4	Llianno	1.6 ± 0.2
	Solhario	2.8 ± 0.3	Filiago	3.0 ± 0.3
	Filiago	3.3 ± 0.3	Tebaldo	3.2 ± 0.5
Border Collie	Caplin	1.5 ± 0.3	Caplin	1.0 ± 0.0
	Lukee	1.8 ± 0.4	Lukee	2.0 ± 0.3
	Ezra	2.3 ± 0.2	Ezra	2.3 ± 0.3
Dingo	Snip	2.0 ± 0.3	Snip	1.3 ± 0.2
	Kean	2.8 ± 0.6	Beri	2.3 ± 0.6
	Ernie	3.3 ± 0.8	Kean	2.8 ± 0.5
	Beri	3.2 ± 0.5	Ernie	3.3 ± 0.4

pickets that were used in this experiment. Neophobia is common in wild canids (Harris and Knowlton 2001; Travaini *et al*. 2013), and most dingoes initially approached the star pickets very cautiously. However, in most cases the test dingoes overcame their caution quickly. The unfamiliarity of the star pickets probably motivated the dingoes to investigate and mark them, presumably to mark them as part of their territory, or perhaps in order to make the objects more familiar (Johnson 1973; Kleiman 1966). Second, the presence of the test urine on the second star picket could have led to a heightened state of alertness and excitement in the test dingoes, leading to a higher rate of investigation and scent marking all throughout the enclosure in response to the unfamiliar intruder, including the star picket containing distilled water. Subtracting the response to control from the response to test urine on a pair-wise basis removed the effect of novelty, and made the comparison between the three urine categories valid.

As expected, the test dingoes' response to the urine of the familiar dingoes was low. The dingoes from which the urine was collected were kept at the same facility as the test subjects; they were housed in kennels next to each other and they used

the same outdoor exercise areas. The test dingoes were therefore already familiar with the dingo urine used in this experiment. The urine of the Border Collie and Maremma males, however, represented marks from unfamiliar canids that the test subjects had never encountered. A higher response of test subjects to the urine belonging to unfamiliar males compared with familiar males was also found for wolves (*Canis lupus*) and Beagles (*Canis familiaris*) (Dunbar and Carmichael 1981; Brown and Johnston 1982). Similarly, the star picket marked with dingo urine likely smelled more familiar than the novel object with distilled water, and therefore warranted less investigation.

Male and female dingoes probably respond differently to the urine of a strange male. While it could signify a potential intruder and threat to both male and female dingoes, for females it could also indicate the presence of a potential mate. For female dingoes there was no consistent difference in their response to the different types of urine. In domestic dogs it has been found that familiar individuals are more likely to be considered as a mate than unfamiliar ones (Daniels 1983), which could be the same in dingoes. This could be the reason why the females quickly and often located the urine from the male dingoes (Variables 1–3). The unfamiliarity of the Maremma and Border Collie males could be the reason why the females investigated their urine longer and were more likely to mark over it (Variables 4–6), as they represented a potential threat.

Both male and female dingoes used standing raised leg urination only, with or without ground scratching, when scent marking the star pickets with urine. Canids can use a range of postures when scent marking (Asa *et al*. 1985; Pal 2003), and females are often recorded using squat urinations (Rothman and Mech 1979; Wells and Bekoff 1981; Sillero-Zubiri and Macdonald 1998). Standing raised leg urination and ground scratching is associated with scent marking by both the male and female of the dominant pair, and often used for demarcation of territorial boundaries (Wells and Bekoff 1981; Sillero-Zubiri and Macdonald 1998; Allen *et al*. 1999). All dingo pairs used in this research were breeding individuals, and their response to the experiment was likely territorial in nature, so the postures could reflect a territorial response. Defaecation was rarely used for scent marking in this study. Other studies have also found low rates of scent marking through defaecation compared with urine marks (Gese and Ruff 1997; Sillero-Zubiri and Macdonald 1998; Allen *et al*. 1999).

Within each urine category, consistent differences were found in the response to the urine of each individual male. For both male and female dingoes, the urine of some males elicited a consistently higher response than others, but the ranking of the individuals was not the same for males and females. It is unclear which attributes of the urine contributed to the strength of the response of the test dingoes. Perhaps it is related to age, rank or health of the individual from which the urine was obtained, the level of hormones in the urine, or perhaps a combination of factors. However, this individual variation could have consequences for working LGDs – some LGDs might be better equipped to engage in olfactory communication with wild predators than others.

The dingoes in this study were kept in captivity, and the response from wild dingoes could be different. However, it seems likely that when working Maremmas scent-mark their territory, dingoes will investigate these marks, and engage in olfactory communication in response. Most species of canid are territorial (Macdonald and Sillero-Zubiri 2004), including domestic dogs (Font 1987; Pal 2003) and dingoes (Thomson 1992; Corbett 2001). Scent marking with scats, urine and ground scratching are used for social communication in all of these species, including advertisement of ownership and territory boundaries (Sillero-Zubiri and Macdonald 1998). As well as responding to the signals left by members of the same species, most canids likely also recognise the social signals left by individuals from other canid species, and can choose to respond to them. For example, Paquet (1991) found that wolves actively investigated coyote (*Canis latrans*) marks, and sometimes over-marked them. Coyotes increased scent marking significantly in response to the presence of wolf marks, and they seemed to react to these marks as they would to intruding conspecifics (Paquet 1991). It therefore seems likely that members of different species would not only be interested in each other's scent marks, but would also recognise and understand each other's territorial signals. Dingoes and domestic dogs are closely related, and it therefore seems likely that dingoes would understand that scent marks left by Maremmas represent the boundary of a territory that is occupied by another canid, even if that canid is not a dingo.

Territorial communication between LGDs and dingoes could lead to territorial exclusion of dingoes from the LGD's area, and therefore from the livestock that are being guarded. Even if trespassing into the LGD's area occurs, individuals are likely fully aware of the fact that they are trespassing. They will therefore change their behaviour in order to avoid detection, as detection can lead to confrontation (Harrington and Mech 1979; Rothman and Mech 1979). This cautious behaviour will mean that trespassing dingoes in Maremmas' territories are unlikely to prey on livestock, as the effort involved with hunting could lead to discovery and confrontation. Therefore, olfactory communication between LGDs and dingoes could greatly aid LGDs in protecting livestock through territoriality. This would likely apply to other canid predators as well.

Acknowledgements

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