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How guardian dogs protect livestock from predators: territorial enforcement by Maremma sheepdogs

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Abstract

Context. Livestock guardian dogs (LGDs, *Canis familiaris*) can be highly effective in protecting livestock from predators; however, how they accomplish this, is poorly understood. Whereas it is clear that these dogs spend a high proportion of their time accompanying livestock, and confront predators that approach closely, it is unknown whether they also maintain territories around the areas used by their livestock and exclude predators from those territories.

Aims. We aimed to determine whether LDG behaviour towards predators is consistent with defence of a larger territory that encompasses the stock, or is based on repelling predators that closely approach livestock.

Methods. We used audio playbacks and scent placements to simulate incursions by dingoes (*Canis dingo*) at different locations with the LDG ranges, and used GPS tracking and automatic cameras to monitor responses to these incursions.

Key results. The LDG responses depended on location of the incursion. When simulated incursions were a significant distance inside the range (about the 50th kernel isopleth), they responded by vocalising, leaving their livestock, and travelling up to 570 m away from the stock to approach the incursion point and display challenging behaviour; when incursions were at the boundary of the range (at or beyond the 90th kernel isopleth), they vocalised but did not approach the incursion point, regardless of the location of the sheep. The LGDs in this study worked in groups. Group members responded differently to simulated incursions, some moving to challenge, whereas others remained close to the sheep.

Conclusions. Our results showed that protection by LGDs extends beyond the immediate vicinity of livestock, and is consistent with the defence of a larger territory.

Implications. If predators are excluded from this territory, LGDs enforce a spatial separation of predators and livestock. This would reduce risk of attack, but also prevents the disturbance and stress to livestock that would be caused by frequent approaches of predators. Where possible, training and management of LGDs should allow them to range freely over large areas so that they can develop and exhibit territorial behaviour, and they should be deployed in groups so that group members can assume complementary roles.

Additional keywords: dingo, human–wildlife conflict, LGD, LPD, predator incursion, territoriality, wild dog.

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Introduction

Livestock guardian dogs (LGDs, *Canis familiaris*) are among the oldest and most numerous of the working-dog breeds (Coppinger and Coppinger 2001). LGDs are raised with stock from an early age, so that they form a strong bond with them (Coppinger and Coppinger 2001; Coppinger and Coppinger 2007). As adults they remain continuously with their livestock and protect them from predators and thieves. By reducing or eliminating livestock predation, LGDs can help resolve predator–livestock conflict, and thereby contribute to predator conservation as well as protecting the livelihoods of livestock producers (Landry 1999; Marker *et al*. 2005*a*, 2005*b*; Urbigkit and Urbigkit 2010).

The effectiveness of LGDs in reducing predation on livestock is well established (see review in Rigg 2001; in addition to Marker *et al*. 2005*a*; Rigg *et al*. 2011; van Bommel and Johnson 2012). However, it is not clear how this is accomplished. Two broad mechanisms could be involved. First, LGDs might provide direct protection by reacting to predators that closely approach their livestock. This reaction could consist of aggressively confronting and driving off predators (McGrew and Blakesley 1982; Lorenz and Coppinger 1986) or otherwise interacting with them in ways that disrupt their hunting behaviour and cause them to seek prey elsewhere (Coppinger *et al*. 1988; Coppinger and Schneider 1995). These behaviours will be most effective in preventing predation if LGDs consistently remain close to their livestock. Second, LGDs might maintain territories, and, by advertising their occupation of territory, deter wild predators from using the area (McGrew and Blakesley 1982). This could be a highly effective form of defence because of its pre-emptive nature and its potential to operate on large scales beyond the immediate locations occupied by stock at a given time. Territorial behaviour would probably be most effective against other canids, because members of the same or closely related species are more likely to recognise each other's territorial signals than those of members of unrelated species. It would require LGDs to spend some time away from their livestock, traversing the territory to maintain advertisement of occupation and police the territory against incursions. Multiple LGDs working together in a group could play complementary roles in maintaining and defending the territory, as well as providing continuous monitoring and protection of livestock.

We used sound and two types of scent experiments to simulate incursions of a wild canid predator (the dingo, *Canis dingo*) in the range of Maremma sheepdogs, and tested the response of Maremmas to these incursions. We expected that if the Maremmas' primary defence of livestock consists of repelling only direct approaches to stock by predators, they would respond to a perceived dingo incursion by moving to their livestock and remaining close to them. In that case, we also expected them to not display any interest in dingo urine scent marks. If, however, Maremmas keep livestock safe by excluding predators from a larger territory around the stock, they should respond to a perceived incursion by leaving the livestock and mounting a challenge at the incursion point. In that case, we also expected them to display a strong interest in dingo urine scent marks, and to leave scent marks in response. In the case of territorial defence, we further predicted that the nature of the response would differ according to the location of the intruders with respect to the range boundary. We expected a strong response for incursions a significant distance inside the range of Maremmas, because this would be more likely to be perceived as an invasion of territory, and a relatively weak response to simulated dingo presence on the range boundary. If the defence of livestock is not based on territoriality but only on direct confrontation of predators closely approaching livestock, we did not expect any response to a simulated incursion at the range boundary, because the distance would be too great for the predator to pose a threat to livestock.

Materials and methods

The research was undertaken under ethics approval from the Animal Research Ethics Committee of the University of Tasmania, approval Number A11886.

Research properties

We worked on two properties in north-eastern Victoria, Australia. Riversdale covered 1214 ha, of which 728 ha was predominantly used for sheep (*Ovies aries*) grazing and supported 1500 merino sheep. Four Maremma sheepdogs guarded all sheep on the property and also visited sheep on two neighbouring properties, particularly during lambing season. Heatherlie covered 2428 ha and ran 6000–8000 merino sheep, along with six Maremmas. On both properties, Maremmas were free ranging, readily crossing stock fences, but generally focusing their movements on their sheep. On Riversdale, a self-feeder in a central location provided Maremmas with *ad lib* dry dog food. The Heatherlie dogs were regularly visited by their owner to be fed. The properties were ~15 km apart and had similar environmental features. They were hilly, with an elevation between ~200 and ~800–900 m asl. Large tracts of uncleared native vegetation remained on both properties and in the surrounding area, mostly comprising grassy dry and wet eucalypt forest. Both properties were surrounded by a mixture of other grazing properties and pine plantations. The regional climate was temperate, with mean monthly temperatures from 4.3°C to 30.9°C, and mean annual rainfall of 693 mm.

Four dogs were studied on each property. In each case, the four (one female and three males) functioned as a social group, although they regularly split up into smaller subgroups or solitary individuals. Two additional dogs on Heatherlie were not included in the study, because of old age in one case and extreme social exclusion in the other. All dogs were desexed.

The main predators in the area were wild dogs (including feral dogs, *Canis familiaris*, dingoes, *Canis dingo*, and hybrids) that had caused large losses of sheep on both properties before introduction of the Maremmas (in 2006 on Riversdale, and 2009 on Heatherlie). Smaller predators, especially red foxes (*Vulpes vulpes*) and wedge-tailed eagles (*Aquila audax*) were also present. In addition to using Maremmas for predator control, trapping, shooting and baiting of wild dogs still occurred in the area. Parts of Heatherlie were bounded by an electrified wild-dog exclusion fence.

Data collection

All Maremmas on both properties were fitted with GPS tracking collars (Telemetry Solutions, Concord, MA, USA) for a minimum of 4 weeks before the start of the experiments. The collars were set to take a location every 30 min, 24 h a day, except that sampling intensity increased during experimental trials (see below). Only locations with a horizontal dilution of precision (HDOP) <4 were included in the analysis. This HDOP value was chosen on the basis of a pilot study, in which all GPS collars were kept stationary on the lower branches of an apple tree for 4 days, taking hourly locations. On the basis of these data, the HDOP value was selected that offered the best balance between filtering out inaccurate locations and data retention. Because of the adequate size of the datasets that were collected, the loss of a small percentage of accurate locations as a result of applying this filter was not considered a problem (Recio *et al*. 2011). In all, 2.1% ± 0.6% (mean ± s.e.) of locations were deleted from each dataset, and the mean HDOP of each remaining dataset was 1.1 ± 0.02. These data were used to calculate a fixed kernel home range (Worton 1989) for each individual dog, and for each group by pooling the tracking data of all members. Autocorrelation does not affect the accuracy of kernel home-range estimates as long as the time interval between successive locations remains constant, and the number of locations is large (De Solla *et al*. 1999); accuracy often improves with a shorter time interval, despite increased autocorrelation (De Solla *et al*. 1999). Therefore, we did not consider autocorrelation to be a problem for our analysis (Reynolds and Laundre 1990; De Solla *et al*. 1999; Fieberg 2007). We used an *ad hoc* smoothing parameter designed to prevent under- or over-smoothing, which involved choosing the smallest increment of the reference bandwidth (Href) that resulted in a 95% home-range polygon that was as contiguous as possible, that is, containing no, or the minimum number of, separate activity areas (Berger and Gese 2007; Jacques *et al*. 2009; Kie *et al*. 2010).

Sound experiment and Scent experiment 1

Playbacks used an Okayo C7180 (Altronic Distributors, Sydney, NSW, Australia) speaker connected to either a Marantz PMD661 (DandM Holdings Inc., Tokyo, Japan) or a Microtrack II (M-audio, Cumberland, MD, USA) digital recorder. The sounds used were either dingo howls, or a boobook owl (*Ninox novaeseelandiae*) call as a control for each simulated incursion. Dingo howling was recorded at the Dingo Research and Discovery Centre, Gisborne, in April 2011, using a Sennheiser ME66 (Sennheiser Electronic Corporation, Old Lyme, CT, USA) microphone and a Marantz PMD661 (DandM Holdings Inc., Tokyo, Japan) digital recorder. Only sound recordings of high quality were used in the playback experiments and no further processing was undertaken on the recordings. The boobook owl calling was obtained from ‘an evening in the Australian bush’ CD (Skeoch and Koschak 2007), because the equipment used to make the recording met the standards set for this experiment.

The speaker and recorders were protected from the weather by placing them in a large black plastic bag, and were camouflaged with an army jacket and natural materials. Playbacks were programmed to start at sunset, and consisted of three 3-min bursts of sound, separated from one another by 5 min of silence. Sound was played at a volume of ~90 db, matching the volume of real-life dingo howling as measured during recording.

On each night that dingo sounds were played, scent marks were also deployed (Scent experiment 1). These consisted of five samples of dingo urine and five of distilled water, each consisting of 1–2 mL. These were placed 20–40 m from the speaker in a line with a spacing of ~4 m, on a bearing likely to be close to the line of approach of the Maremmas. The likely line of approach was determined by the location of the Maremmas at the time the equipment was set up, and the topography of the landscape (i.e. such as rock formations, dense shrubbery). The scents were grouped together by treatment; the order of the treatments was random. Covert II (DLC Trading Co, Lewisburg, PA, USA) motion-triggered cameras were set up to capture the behaviour of Maremmas at each scent mark, and around the speaker.

On nights when trials were conducted, the schedule of the GPS collars was changed to taking a location every 2 min, starting 15 min before the first playback and continuing for 75 min to collect detailed data on the Maremma movements during the experiment. It then returned to the standard schedule. Three digital voice recorders were spread through the general area where the Maremmas spent most of their time, and were left recording throughout the day and the night of the playbacks to record any barking of Maremmas and as a check that the speaker had functioned correctly. On Heatherlie, the trials were observed with binoculars from a distance, whereas on Riversdale, this was not possible. All equipment was set up in the morning of the day of the playback, and all reasonable care was taken to prevent the Maremmas from noticing the activities, and to limit the spread of human scent around the area.

The incursions were simulated at the following two different distances relative to the centre of activity of each group’s area of use: between the 45% and 55% contour lines of the kernel-density distributions (‘near’ trials), and between the 90% and 100% contour lines of the kernel-density distributions (‘far’ trials). In ‘near’ trials, the speaker was located between 10 and 400 m away from the sheep at the time of the playback; in far trials, this was between 10 and 1400 m (Fig. 1). In only one ‘near’ playback on each property, and one ‘far’ playback on one property, the sheep closely approached the speaker just before the start of the experiment (10-m distance from the speaker). Experiments were undertaken in blocks of five consecutive days, consisting of one simulated incursion (dingo howling and scents) and one control (Boobook owl calling) at each of the two distances, with 1 day without playback separating the experiments at the two distances. The order of the experiments was randomised in a balanced design with regard to distance (near vs far) and sound (test vs control). Blocks of experiments were at least 2 days apart. The experiments were repeated four times with the Maremmas on Riversdale between January and March 2012, and five times with the Maremmas on Heatherlie between July and September 2012. At each repetition, a different sound recording was used of both dingo howling and Boobook owl calling.

Scent experiment 2

After these trials were completed, an additional scent experiment was conducted. Four 2.25-ha areas were chosen in the same kernel-density distribution contour lines as defined for the playback experiments, with two pairs at each distance. One of each pair was randomly assigned as a control, and the pairs were separated by a minimum of 100 m. For the test, the researcher walked the boundary of the area and deposited a 1-mL dingo-urine scent mark approximately every 3 m. The procedure was the same for the control area, but distilled water was used to mark the boundary. Natural boundaries such as fence lines or forest edges

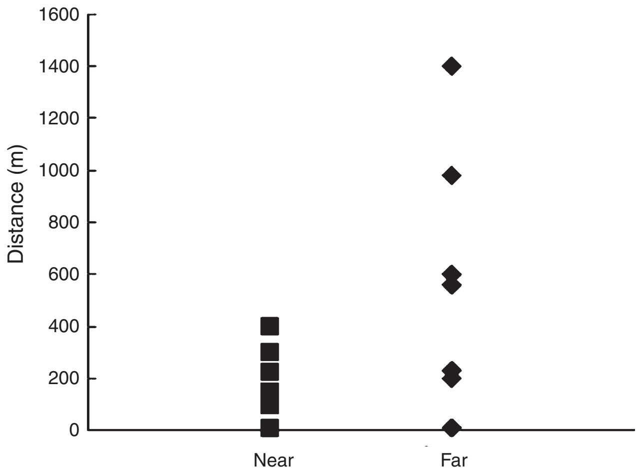

Fig. 1. Distances of sheep from the location of the simulated wild-dog incursion in all experiments.

were followed where possible. The GPS collars of the Maremmas were set to take a location every 15 min for 2 weeks following the depositing of the scents.

Data analysis

In some simulations, all Maremmas were in a location from which it was impossible for them to have heard the howling, because of the topography of the landscape (i.e. they were located on the opposite side of a high ridge-line, with a directional speaker aimed away from them). These cases were excluded from the analysis, leaving three repeats from Riversdale and four repeats from Heatherlie for analysis.

Sound experiment and Scent experiment 1

Simulated wild dog incursions and sound controls were analysed in two ways. First, 15 variables defining the immediate response of each individual Maremma at the time of the playback were measured with regard to the sound and scent (Table 1). For the variables that were derived from the GPS-collar data, a mean number of 24 ± 2.2 locations was used per dog, with a mean HDOP of 1.0 ± 0.02, measuring the response from the start of the playback until the end. Because there was never any response to the control playback, analysis was undertaken only on the variables measured for the test playback. Each variable was entered as the dependent variable in a linear mixed model, with dog identity nested in property as a random effect, and the following variables as fixed effects: (1) dog sex, (2) distance of playback (near vs far), (3) repetition number of the playback and (4) distance of the sheep to the playback location. For each dependent variable all possible combinations of fixed-effect variables were modelled, with one exception; Variable 2 (distance of playback) was correlated with Variable 4 (distance of the sheep to the playback location) (Spearman correlation: $rho = 0.50$, $n = 57$, $P < 0.001$); therefore, these two variables were never included in the same model. The models were ranked according to their Akaike information criterion (AIC) weight (Burnham and Anderson 2002). We considered all models that fell within 2 ΔAIC of the top model to be reasonable descriptors of the data. In Scent experiment 1, the scent was often not found (in 10 of 14 occasions) and if it was found, it was often only by one dog. Distilled water never elicited any response. Therefore, only Variable 8 (Table 1) could be included in this analysis. Observations of the playback experiments at Heatherlie are described where they give additional information not captured by the equipment.

Table 1. Variables measured to record the immediate response of each individual Maremma during trials

Variables measured for individual Maremmas at the time of each trial	
1	Presence or absence of any response
2	Presence or absence of barking
3	Presence or absence of movement in the direction of the speaker
4	Latency until start of barking (measured from the time the playback started)
5	Latency until start of movement
6	Distance moved towards the speaker (in percent of total distance, measured between the location of the speaker and the starting location of the Maremma)
7	Speed of movement
Variables measured for individual Maremmas regarding their response to scent at a test trial	
8	Whether or not a dog located any dingo urine scent marks
9	Whether or not a dog located any water scent marks
10	Number of dingo urine marks found
11	Time spent sniffing each mark, and the average sniffing time per mark
12	Number of scent-marking behaviours in response to the dingo urine
13	Number of water marks found
14	As Variable 11, but for water
15	As Variable 12, but for water

Second, to investigate whether the dogs' response continued longer than the immediate reaction to the trials, for each individual Maremma, the following variables were calculated for each night and day in the 24-h period following the playback: (1) the average speed of movement (m h^{-1}) and (2) the average position within the kernel isopleths (in each 10% increase in the kernel distribution). Night was defined between the end of the playback and sunrise the next day, day was defined between sunrise and sunset the day after the playback. The mean number of locations used in these 24-h calculations was 45 ± 0.8 per dog per trial, with a mean HDOP of 1.1 ± 0.008. The analysis was the same as for the immediate response variables, with one additional explanatory variable: sound (dingo vs owl), and one additional random variable: time of day (day vs night).

Scent experiment 2

For Scent experiment 2, the following variables were measured for each area for each individual dog for the 2 weeks following the laying of the scent: (1) the number of visits by the Maremma to the area enclosed by the scent boundary and (2) the number of visits to the scent boundary itself (area within 10 m of the boundary). A paired Student's *t*-test was used to test for differences between test and control for both variables, and for differences between areas 'near' and 'far'. One dog on Heatherlie was excluded from the analysis, because the location of the scent areas was too far removed from the 50% and 95% kernel isopleths of the individual dog.

Means ± s.e. are given. Statistical tests were two sided with a 95% confidence level. All spatial analyses were performed using the geospatial modelling environment (Beyer 2012) and ArcGIS 10 (ESRI 2011); all statistical analysis were performed using PASW Statistics 18 (SPSS Inc. 2009).

Results

Maremma ranges

On both properties, the entire home range (99% kernel isopleth) of the Maremmas encompassed all the sheep-grazing paddocks, and extended up to 2 km beyond them, except for one sheep paddock on Heatherlie (Fig. 2). On Heatherlie, the 95% kernel isopleths covered on average 879 ± 41 ha. The core 50% of the dogs' home range covered on average 157 ± 19 ha and centred on the main areas of the main sheep paddocks (Fig. 2*a*). On Riversdale, the 95% kernel isopleth covered on average 148 ± 46 ha. The core 50% of the Maremmas' home range covered on average 11 ± 3 ha and centred on the self-feeder,

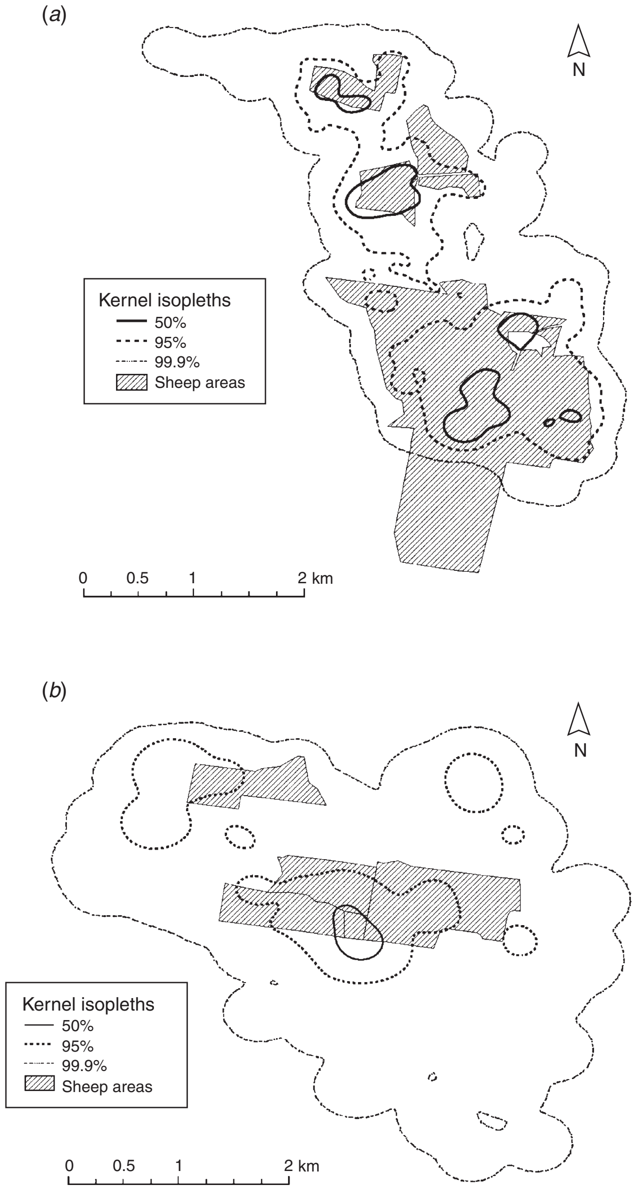

Fig. 2. 50%, 95% and 99.9% group kernel isopleths of Maremma group home ranges in relation to the sheep paddocks on (*a*) Heatherlie and (*b*) Riversdale.

and encompassed parts of the main paddocks that contained sheep at the time of the experiment (Fig. 2*b*). Maremma activity was strongly concentrated within the 10% kernel isopleth of their range (Fig. 3).

Responses to playbacks

Maremmas never responded to the control playback, whereas they always responded to the test playback. In Scent experiment 1, distilled water never elicited any response even if found, whereas dingo urine always elicited a reaction if found. Maremmas were usually located in the 10% core area of their home range at the start of trials.

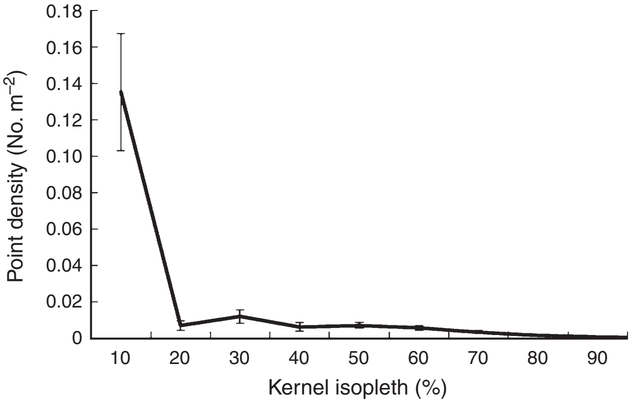

Fig. 3. Mean (± s.e.) density of GPS tracking locations within each kernel isopleth, from all dogs on both properties.

Immediate response

Individual dogs differed in their response during a playback experiment, in ways that were consistent across experiments. One individual raised the alarm, one or two led the charge (if there was one), and one or two usually lagged behind, staying closer to the livestock. Variables 1 and 2 (presence or absence of any response and of barking, Table 1) could not be analysed as the response was always 100%: Maremmas always barked and/or howled in response to a test trial.

Playbacks performed 'near' provoked greater responses than playbacks performed 'far'. This was regardless of the location of the sheep relative to the speaker at the start of the experiment; the explanatory Variable 4 (distance of sheep to playback location) was never present in the best models, whereas the explanatory Variable 2 (distance of playback) was always present (Table 2). When the experiment was undertaken 'near', the Maremmas usually barked immediately and charged towards the speaker, often travelling the full distance to the speaker in a relatively short time (Table 3). When undertaken 'far', the Maremmas always barked, but in most cases this was after some time had passed since the start of the playback (Table 3). They usually did not move in the direction of the speaker, and if they did, it was never the full distance (Table 3).

Males and females differed in their response to the playbacks; the variable sex was often included in the best models (Tables 2, 3). The females in the present study moved towards the sound more often, and earlier, than did the males, but the males barked earlier than the females (Table 3). With an increasing number of repetitions, some habituation seems to have occurred. Maremmas took longer to start barking, and they were less likely to move towards the speaker. If they did move in the direction of the speaker, it was after increasingly more time had passed since the start of the experiment, and they moved shorter distances at a slower pace.

In one 'near' dingo playback trial on Heatherlie, only three Maremmas were present on the side of the property where the trial was undertaken, and one male was ~6 km away. The data from his GPS collar showed that soon after the trial started, he began moving in a straight line towards the other Maremmas, where he arrived just after the end of the trial.

Table 2. The models within 2 ΔAIC of the top-ranked model for each immediate response variable and each longer-term response variable that was measured during the playback experiments

Variable measured	Explanatory variables included in the model	AIC	ΔAIC	AIC weight	Model likelihood
Immediate response					
Presence or absence of movement	Distance	67.8	0	1	0.4
	Distance, dog sex	68.4	0.6	0.7	0.3
	Distance, repetition	69.3	1.5	0.5	0.2
Latency until start of barking	Distance, dog sex, repetition	699.0	0	1	1.0
Latency until start of movement[A]	Dog sex, repetition	309.4	0	1	0.8
Distance moved	Distance, dog sex, repetition	282.7	0	1	0.9
Speed of movement	Distance, dog sex, repetition	581.2	0	1	0.9
Dingo urine scent marks located or not	Distance	44.1	0	1	0.4
	Distance, dog sex	44.5	0.5	0.8	0.4
	Distance, repetition	45.0	1.0	0.6	0.2
	Distance, dog sex, repetition	45.9	1.8	0.4	0.2
Longer-term response					
Speed of movement	Distance, dog sex, repetition, sound	2965.8	0	0.9	1.0
Location in kernel isopleths	Distance, dog sex, repetition, sound	1991.2	0	0.5	1.0

[A] Only 'near' distance could be analysed, because there were not enough data to include the 'far' distance; Maremmas often did not move at all at the 'far' distance.

Table 3. The differences in the categories of the explanatory variables 'distance' and 'dog sex' for each immediate response variable entered in the generalised mixed models

Immediate response variable	Distance		Dog sex	
	Near	Far	Male	Female
Presence or absence of movement	Movement towards speaker: $n = 25$ of 29 (86%)	Movement towards speaker: $n = 10$ of 27 (37%)	Movement towards speaker: $n = 24$ of 40 (60%)	Movement towards speaker: $n = 11$ of 15 (73%)
Latency until start of barking	Mean time: 46.4 ± 24.4 s; immediate barking: $n = 16$ of 28 (57%)	Mean time: 183.8 ± 56.1 s; immediate barking: $n = 10$ of 26 (38%)	Mean time: 103.4 ± 33.3 s; immediate barking: $n = 17$ of 39 (44%)	Mean time: 136.3 ± 72.4 s; immediate barking: $n = 9$ of 15 (60%)
Latency until start of movement	Mean time: 83.8 ± 17.1 s; movement within 10 s: $n = 21$ of 25	Not enough data to analyse	Mean time: 65.9 ± 35.6 s ($n = 24$); movement within 10 s: $n = 21$ of 24	Mean time: 51.5 ± 47.7 s ($n = 11$); movement within 10 s: $n = 10$ of 11
Distance moved	Mean distance: 72.0% ± 6.2% ($n = 29$); 263.0 m ± 31.9 m ($n = 29$); max distance: 576 m (100%)	Mean distance: 11.6% ± 8.1% ($n = 27$); 108.9 ± 33.8 m ($n = 27$); max distance: 570 m (59%)	Mean distance: 42.3% ± 7.0% ($n = 40$); 184.5 ± 30.9 m ($n = 40$)	Mean distance: 42.6% ± 11.0% ($n = 15$); 205.3 ± 44.0 m ($n = 15$)
Speed of movement	Mean speed: 86.7 ± 12.6 m min^{-1} ($n = 29$)	Mean speed: 13.0 ± 3.6 m min^{-1} ($n = 27$)	Mean speed: 51.2 ± 10.2 m min^{-1} ($n = 40$)	Mean speed: 51.2 ± 15.5 m min^{-1} ($n = 40$)
Dingo urine scent marks located	10 of 29 located (34%)	0 of 28 located (0%)	9 of 43 located (21%)	1 of 14 located (7%)

Response to scent during playbacks

Distance, dog sex and repetition were all included in the top models explaining whether dingo urine marks were found by the Maremmas or not. Scent was never found in 'far' trials, only in the 'near' trials (Table 3). Males were more likely to find scent marks than were females (Table 3), and Maremmas were less likely to find the scent with an increasing number of repetitions.

Data from the GPS collars showed that when a playback started in 'near' trials, the Maremmas usually moved towards the speaker first, apparently too intent on the sound to locate the scent marks. If marks were found, it was after the playback had finished; however, often they returned to the sheep via a different route, missing the marks altogether. If a dingo urine mark was found, it was always sniffed by the Maremma, with an average sniffing time of 22.7 ± 6.4 s. Barking near the scent was also observed on the cameras. Marking directly over dingo urine marks was caught on camera for three male Maremmas, on one occasion each.

Long-term response

The explanatory variables distance, sound, dog sex and repetition number were all included in the top models for the dependent variables speed of movement and location in kernel isopleths in the 24 h after a trial (Table 2). In the 'far' trials, speed of movement was lower in the 24 h after the trial, and the Maremmas stayed closer to the centre of their home range than they did in the 'near'

Table 4. The differences in the categories of the explanatory variables 'distance', 'sound' and 'dog sex' for each longer-term response variable entered in the generalised mixed models

Explanatory variable	Longer-term response variable Speed of movement	 Kernel location
Distance		
Near	Mean speed: 261.9 ± 22.3 m h^{-1} (n = 115)	Mean isopleth: 45.5 ± 2.2 (*n* = 111)
Far	Mean speed: 176.7 h ± 13.3 m h^{-1} (n = 110)	Mean isopleth: 43.1 ± 2.3 (*n* = 112)
Sound		
Dingo	Mean speed: 234.8 ± 21.7 m h^{-1} (*n* = 114)	Mean isopleth: 44.6 ± 2.2 (*n* = 114)
Owl	Mean speed: 205.3 ± 15.5 m h^{-1} (*n* = 111)	Mean isopleth: 44.0 ± 2.3 (*n* = 107)
Dog sex		
Male	Mean speed: 207.4 ± 14.5 m h^{-1} (*n* = 165)	Mean isopleth: 44.7 ± 1.8 (*n* = 162)
Female	Mean speed: 260.7 ± 30.4 m h^{-1} (*n* = 60)	Mean isopleth: 43.2 ± 3.2 (*n* = 59)

trials (Table 4). Speed of movement was higher and the dogs spent more time near the periphery of the range following a dingo playback than following the control playback (Table 4, Fig. 4). Males had a lower speed of movement, and tended to move closer to the periphery of their range than did the females (Table 4). With increasing repetition, speed of movement increased and Maremmas tended to spend more time towards the periphery of their range in the 24 h after a trial.

Behaviour observations

Direct observations on Heatherlie showed that when the playbacks of dingo howling began, the sheep startled, flocked together, and moved away from the sound. This process was often aided by the Maremmas; one or two dogs would run up and down past the sheep on the side from which the sound came, and in some cases actively seemed to herd the sheep away, whereas the others stood among the sheep and barked. In one instance, a dog left the flock and his companions and ran in the general direction of the speaker for ~100 m, where he roused a lamb that had been asleep in the grass and chased it back to the flock. In general, the sheep were sent on their way in a relatively short time, after which the Maremmas would leave them and moved in the direction of the speaker. Direct observation of response to dingo scent marks occurred only once for one male. This dog did not mark directly over any scent, but scent-marked ~1 m away from the dingo urine marks. On Heatherlie, during all experiments, all male Maremmas that could be observed started scent-marking the moment they responded to the sound, often at the same time as they started barking. The marking was performed with a high frequency, mostly aimed at vertical objects.

Scent experiment 2

At the 'far' distance, the areas enclosed by the scent, or the scent boundary, were never visited either for the test or control plots. At the 'near' distance, the overall number of visits was relatively small. For the area enclosed by the scent, the mean number of visits to the test area was 4.3 ± 1.0, and to the control area it was 0.9 ± 0.4. The mean number of visits to the test boundary was 3.4 ± 0.6, and to the control boundary it was 0.7 ± 0.2. At the 'near' distance, the areas enclosed by the dingo urine received significantly more visits from Maremmas than did the areas enclosed by the control (paired Student's *t*-test: $t = 3.0$, $n = 7$, $P = 0.02$), on average 3.7 ± 1.0 times more. The dingo urine-scent boundary also received significantly more visits from Maremmas than did the control-scent boundary (paired Student's *t*-test: $t = 4.0$, $n = 7$, $P = 0.01$), on average 3.4 ± 0.6 times more.

Discussion

The Maremmas in our study always responded actively to simulated incursions on their range by dingoes. When incursions were some distance inside their range, they moved up to 570 m away from their sheep to challenge the perceived intruder. When the incursion was on the range margin, the Maremmas vocalised and scent-marked but did not move out to challenge the intruder, even though in some cases this perceived intruder was relatively close to sheep. This is similar behaviour to that shown by territorial canids such as wolves and coyotes in response to incursions into their territory (Harrington and Mech 1979; Mech and Boitani 2003). If the Maremmas had not been territorial but had predominantly operated by confronting predators that closely approach stock, they would have remained close to the livestock so as to repel any direct attacks, and would not have travelled away from them to challenge a perceived intruder. The Maremmas would then also not have responded to a perceived predator at the edge of their range if this predator was a great distance removed from the sheep, because this predator would not have presented any direct threat to the livestock. In addition, in the cases where the incursion at the edge of their range was close to sheep, the Maremmas would have travelled the whole distance to the sheep closest to the perceived threat, so as to repel that threat. The nature of the response and the differences according to the location of the incursion suggest that the Maremmas treated at least a central part of their range as a territory, and responded to invasion of this territory similarly to wild canids (Bekoff and Wells 1986; Mech 1993, 1994; Gese 2001; Mech and Boitani 2003; Parker 2010).

The observation that male Maremmas scent-marked with high frequency in response to the simulated incursions suggests signalling of territory occupation to potential intruders. Territorial arctic foxes (*Alopex lagopus*) also scent-mark and bark while approaching playback vocalisations at the edge of their territory (Frommolt *et al*. 2003). However, the dingo urine placed near audio playbacks was often not located. Possibly, the experimental design did not simulate a real-life incursion

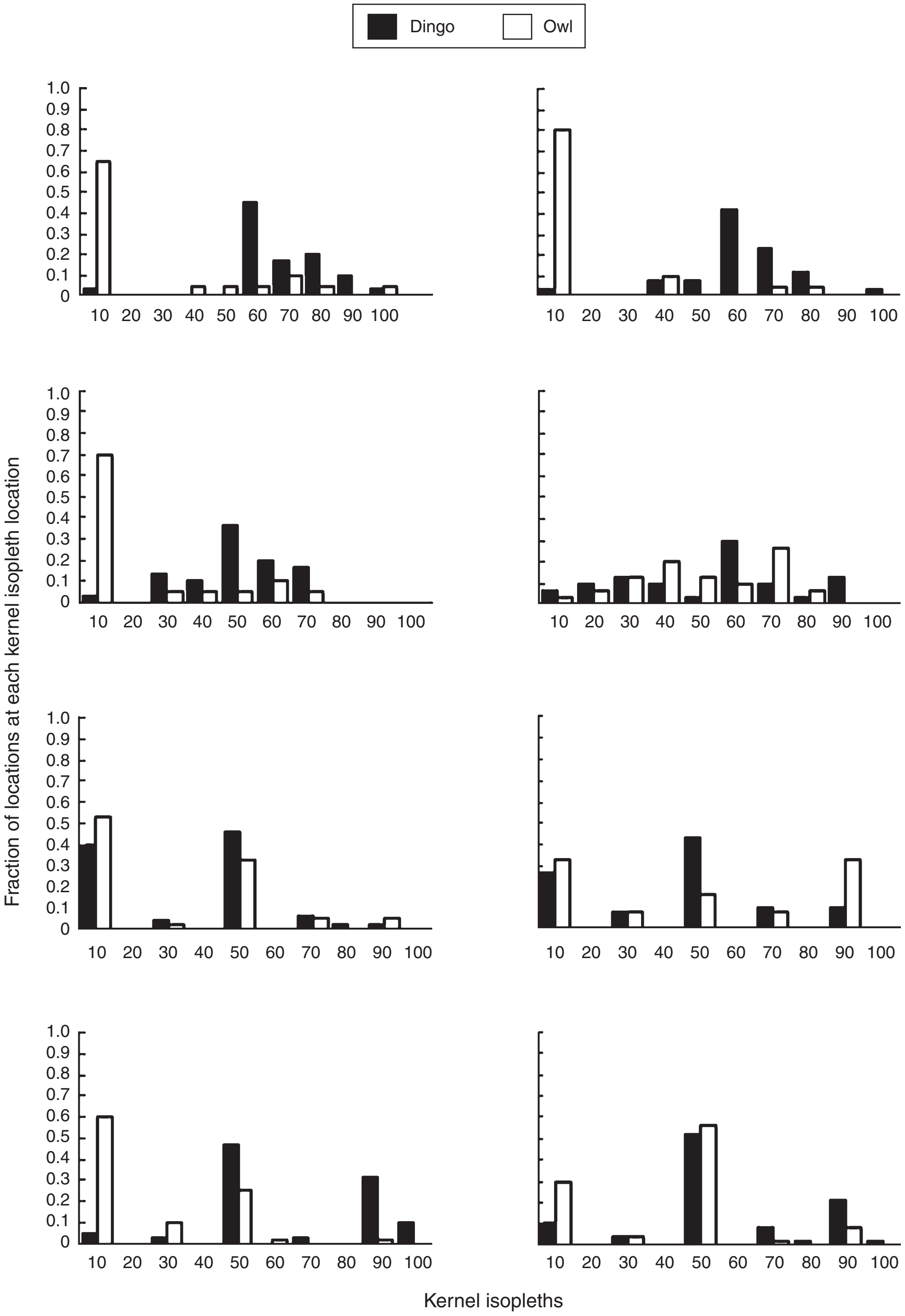

Fig. 4. The distribution of locations within the home range where Maremmas spent their time at night following the trials at the 50% kernel isopleth. On Riversdale, three test and three control trials are included in the analysis (10 locations per night); on Heatherlie, four test and four control trials are included in the analysis (12 locations per night). The top four Maremmas were from Riversdale, the bottom four from Heatherlie. The top-left graph is the Riversdale female, and the bottom-left graph is the Heatherlie female.

accurately with regard to scent. Canids leave scent trails that consist of more than single urine marks, for example, from shed skin cells or fur (Bradshaw and Nott 1995). The absence of such a scent trail in combination with the presence of human scent might explain the low discovery rate. Even when found, dingo urine was not often over-marked by Maremmas. However, because of the limited field of the cameras used to detect this behaviour, marking could have gone unrecorded if performed some distance away from the actual dingo urine.

In the experiment that deposited scent trials without an associated playback of howling (Scent experiment 2), scent was never found when placed at the periphery of the Maremma range, possibly because this was outside the area treated as a territory. Scent trails placed within the range were visited more often than control sites. Similar behaviour has been recorded in coyotes and red foxes (Shivik *et al*. 1996; Gese and Ruff 1998; Arnold *et al*. 2011), and is consistent with territoriality, because scents from potential intruders should be investigated. The higher activity further away from the core of the home range in the 24 h after a 'near' test trial compared with a 'far' test trial would also indicate a higher level of arousal in the Maremmas following a 'near' incursion. This could have involved checking for signs of intrusion, and patrolling the territorial boundary.

We saw evidence that Maremmas provide each other with backup in the case of a predator incursion, and found consistent individual differences among the Maremmas in their behaviour in response to the trials. The first response of some Maremmas seemed to be to attend to their sheep, which would facilitate direct defence of the stock in the case of a real attack. However, the behaviour of the Maremmas that resulted in the sheep moving away from the threat could also be a by-product of running up and down by the Maremmas in general excitement. The dogs displaying this behaviour always subsequently left the sheep, and moved away from them to actively challenge the perceived intruder, even if this intruder was quite far removed from the sheep (up to 570 m). It is unclear how the roles were divided between the individual LGDs, but perhaps age, rank or sex played a part. Differences were found in responses between males and females, but the sample size for females was quite small in the present study. In wolves and coyotes, it is mostly the dominant individuals that are involved in territorial advertisement and defence, whereas submissive individuals participate at a much lower rate or not at all (Bekoff and Wells 1986; Mech 1993, 1994; Gese 2001). The overall response of the Maremmas in this experiment seemed to decrease with an increasing number of repetitions, likely owing to habituation. Recorded sounds are never exactly the same as sounds produced by live animals, and Maremmas could have learned to recognise this difference.

Outside of simulated predator incursions, the Maremmas in the present study also displayed behaviour consistent with territoriality, such as regular barking, scent-marking and boundary patrolling (L. van Bommel pers. obs.). In wild animals, territories give exclusive, or priority, access to resources such as food or refuge, which are important for the animals' fitness, survival and reproduction (Burt 1943; Mech and Boitani 2010). For the Maremmas in the present study, the resources crucial for survival and fitness were provided by their owners, and they could not reproduce. The motivation for territorial behaviour is therefore likely of a social nature. The way LGDs are raised ensures that there is a close bond between the LGDs and their livestock (Coppinger and Coppinger 2001), making the stock a valuable resource for the LGDs; territoriality is an efficient way to protect this resource. The livestock husbandry system could influence the effectiveness of LGD territorial behaviour. Traditionally, in many societies, migratory livestock husbandry is practiced, which precludes the LGDs from establishing a stable territory. This could make territorial behaviour less effective, and the LGDs would be likely to rely more heavily on other behavioural mechanisms, such as direct confrontation of predators, to keep livestock safe. However, in many countries including Australia, pastoral farming is the most common animal husbandry system. In pastoral farming, livestock are relatively sedentary. Movement of stock occurs during paddock rotation; however, overall, the livestock are confined within the boundaries of the land managed by the farmer. This enables resident LGDs to have a stable, spatially defined territory, and use territoriality to protect their livestock.

However, for territorial exclusion to work, predators also need to recognise and respect the territorial boundaries of LGDs. Dingoes and other wild dogs exhibit territorial behaviour (Thomson *et al*. 1992; Corbett 2001; Robley *et al*. 2010) and, being members of the same species, wild dogs and guardian dogs ought to recognise each other's territorial signals. Territorial boundaries will exclude conspecifics; however, in many species, trespassing in others' territories does occur for a variety of reasons (Peterson *et al*. 1984; Messier 1985; Fuller 1989; Thomson 1992; Shivik *et al*. 1996; Sacks *et al*. 1999). It therefore seems likely that wild dogs trespass in Maremmas' territories as well, as found by Allen (2012) who recorded dingoes moving through Maremma paddocks (although without preying on sheep). Trespassers are probably fully aware that they are trespassing, and change their behaviour to avoid detection and the confrontation that would follow (Harrington and Mech 1979; Rothman and Mech 1979). This cautious behaviour will mean that trespassing wild dogs or dingoes in Maremmas' territories are unlikely to prey on livestock, as the effort involved with hunting would probably lead to discovery and confrontation.

Territorial behaviour by LGDs extends protection against predators to areas beyond the immediate location of the livestock. In this way, LGDs not only reduce predation, but also reduce the stress on livestock (as well as their owners) that would be caused by frequent predator incursions. In addition, lethal forms of predator control are probably reduced when LGDs are used (van Bommel 2010), as is the risk of retaliation by farmers in response to frequent predator disturbance of livestock. This can contribute to the conservation of wild predator species (Landry 1999; Marker *et al*. 2005*a*, 2005*b*; Urbigkit and Urbigkit 2010).

To fully benefit from territorial predator exclusion, training and management of LGDs should be aimed towards allowing them to range freely over areas beyond the location of the livestock, and they should be deployed in groups so that individuals can assume complementary roles. Obviously, this management style will not always be possible. In more densely populated areas or on smaller properties, dogs roaming outside of livestock paddocks, and therefore property boundaries, can lead to accidents. However, free ranging of LGDs is already successfully used on large Australian properties where wild dogs are the main threat to livestock (van Bommel 2010; van Bommel and Johnson 2012). In general, as long as a property is large enough to accommodate a LGD range (which can be >897 ha), it should be feasible to use this management system.

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