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RESEARCH ARTICLE

Livestock guardian dogs establish a landscape of fear for wild predators: Implications for the role of guardian dogs in reducing human–wildlife conflict and supporting biodiversity conservation

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Abstract

1. Livestock guardian dogs (LGDs) are increasingly used to protect livestock from predators, but their effects on the distribution and behaviour of wild predators are mostly unknown. A key question is whether LGDs exclude predators from grazing land, or if predators continue to use areas with LGDs but modify their behaviour in ways that reduce impacts on livestock.
2. We studied effects of LGDs (Maremma sheepdogs) on distribution and behaviour of red foxes *Vulpes vulpes* in north-eastern Victoria, Australia. We mapped the activity of LGDs across the study areas using GPS tracking and measured fox activity using remote cameras. We also measured risk-sensitive foraging in foxes to test if they reduced feeding time at sites regularly used by LGDs.
3. Foxes occurred throughout areas occupied by LGDs, but their probability of detection was negatively related to the probability of LGD presence. Foxes extracted fewer food items from experimental food stations in proportion to the intensity of local activity of LGDs. This indicates that, though foxes overlapped with LGDs, they responded to risk of encountering LGDs by allocating less time to foraging.
4. While LGDs do not necessarily exclude wild predators from areas used for livestock production, they can have strong effects on predator behaviour. Reduction in time allocated to foraging in areas regularly used by LGDs could lead to suppression of hunting behaviour and therefore a reduction in attacks on livestock. The flexible response of predators to LGDs should facilitate coexistence of wild predators with livestock farming, by allowing predators to continue to use areas occupied by livestock while still preventing attacks on those livestock. Our results therefore strengthen the case for use of LGDs in the conservation of predators threatened by conflict with farming. Suppression of hunting behaviour should also mean that prey species experience reduced rates of predation on farmland

with LGDs. This effect could be valuable for conservation of threatened species of prey.

KEYWORDS
giving-up density, livestock protection, LPD, mesopredator, predator control, retaliatory killing, threatened species

1 | INTRODUCTION

Livestock Guardian Dogs *Canis familiaris* (LGDs) are working dogs that accompany livestock and protect them from attacks by predators. Use of these dogs has ancient roots in southern Europe and central Asia (Gehring et al., 2010; Ivaşcu & Biro, 2020; Welker et al., 2022), but declined in the 20th century. Recently, use of LGDs has been revived and adopted in many parts of the world. LGDs are often highly effective in reducing losses of livestock to predation (Marker et al., 2005; van Bommel & Johnson, 2012; van Eeden et al., 2018). Their use can therefore support conservation of threatened predators by reducing retaliatory killing by farmers. In southern Africa, for example, farmers with LGDs are less likely to kill cheetahs *Acinonyx jubatus* and leopards *Panthera pardus* than are farmers without LGDs (Potgieter et al., 2016; Whitehouse-Tedd et al., 2020).

Despite the evident value of LGDs in the management of human–wildlife conflict, we know little about how they interact with predators and what effects these interactions have on predator behaviour. It is clear that LGDs spend much of their time close to their livestock and that they confront and drive off predators that approach livestock (Landry et al., 2020; van Bommel & Johnson, 2014a). Otherwise, attacks on wild predators by LGDs are apparently rare, and killing of predators by LGDs is rarer still (Johnson et al., 2019; Potgieter et al., 2016; Smith et al., 2020; Whitehouse-Tedd et al., 2020).

Although they spend much of their time escorting livestock, LGDs may range over large areas (van Bommel & Johnson, 2014b) and advertise their presence by scent-marking and barking loudly. Experiments in Australia showed that some LGDs left their sheep flocks to challenge simulated incursions of dingoes *Canis dingo* on the boundaries of their ranges (van Bommel & Johnson, 2014a). Similarly, observations of interactions between LGDs and wolves *Canis lupus* in France showed that the LGDs not only repelled predators that closely approached their sheep flocks but also challenged and pursued wolves that entered the LGDs' ranges (Landry et al., 2020).

These behaviours of LGDs could have two distinct effects on the distribution and behaviour of predators. First, they could result in interspecific territorial exclusion, such that predators rarely encroach on ranges occupied by LGDs. This would be especially the case if, as well as being expelled from LGD territories, predators recognise the boundaries of LGD territories and avoid crossing them. Territorial exclusion would be desirable for livestock protection, but potentially harmful to the status of threatened predators, because widespread use of LGDs could deny those predators access to significant areas of habitat and the non-livestock prey resources they contain.

Second, predators might enter LGD ranges but respond to the risk of encountering LGDs by modifying their behaviour. In natural systems, interference interactions from top predators pose a risk to smaller predators, which creates a landscape of fear (Gaynor et al., 2019). Most predators are capable of assessing and responding to environmental risk cues, and will alter their behaviour to reduce this perceived risk (Haswell et al., 2018). Risk avoidance in a landscape of fear can include spatial or temporal avoidance of the top predator to avoid fine-scaled overlap in habitat use, or behavioural changes such as increased alertness and a reduction in hunting behaviour (Gaynor et al., 2019). LGDs could create a landscape of fear for other predators in agricultural landscapes, and the resulting suppression of these predators' hunting behaviour could lead to reduced predation rates, both on livestock and on wildlife species that overlap with LGDs.

This study tested the effects of LGDs on distribution and foraging behaviour of red foxes *Vulpes vulpes* on large farms in north-eastern Victoria, Australia. We used GPS-tracking to map spatial variation in the intensity of use of each study area by LGDs and tested whether the probability of detection of foxes on remote camera traps was negatively related to the intensity of use by LGDs. Also, we used the measurements of feeding activity by foxes at artificial feeding stations to describe risk-sensitive foraging by red foxes. This used a giving-up-density (GUD) experiment, in which foxes were able to gain food by remaining at a site, but in a way that demanded an increasing cost in time and sacrifice of vigilance, and which would therefore entail higher risk. We predicted that foxes would feed less at sites with higher intensity of use by LGDs, indicating a reduced willingness to forage in response to risk, which could translate into a suppression of hunting behaviour in response to risk.

2 | MATERIALS AND METHODS

2.1 | Study sites

We worked on four properties in north-east Victoria, Australia; two used as experimental sites and two as controls. Annual rainfall in the region is 691 mm and mean temperatures range from 4.1 to 12.3°C in winter and 16.6 to 31.0°C in summer. The main predators of livestock were red foxes, and dingoes and feral dogs *Canis familiaris*. No alternative control of predators was undertaken in the areas used by LGDs, but in the surrounding areas, lethal control continued by way of trapping, shooting, and poison baiting.

The two experimental properties ran sheep and cattle, with Maremma sheepdogs (hereafter, Maremmas) guarding the sheep. Riversdale had a total area of 1214 ha, of which 350 ha was used to graze 1000 merino sheep with three Maremmas; a neighbouring 176-ha property was almost fully enclosed by the boundaries of Riversdale and ran similar livestock, so was included in the Riversdale site. Heatherlie was a 3200-ha property, of which 2100 ha was used to run 6000 crossbred sheep with four Maremmas (including one old dog who was working only part-time). The Maremmas on both properties ranged freely, functioning mostly as a single social group using a common home range on each property. They readily crossed stock fences and their ranges extended beyond those of their sheep. Both experimental properties were hilly (elevation from ~200 to 900 m a.s.l.) with large tracts of uncleared native vegetation. They were 10 km apart and surrounded by a mixture of other grazing properties, native forest and pine plantations. Heatherlie was partly bounded by a wild dog exclusion fence.

The two control sites were on properties that did not use LGDs but were otherwise similar to the study areas. Wagonbark covered 1416 ha and ran sheep and cattle. A 530-ha area within this property, mostly running sheep, was used as a control site. Wagonbark did not practice systematic predator control, but its neighbours conducted lethal control. Mullameah covered 1821 ha, with sheep and cattle on a 1240 ha area, which was partly enclosed by a wild dog exclusion fence. Poison baits were distributed four times per year in locations that were perceived to be predator problem areas.

Each experimental site was paired with its own control site (Riversdale and Wagonbark, 10 km apart; Heatherlie and Mullameah, 45 km apart) due to the fox survey and experiments taking place in different seasons for each pair of properties; fox activity and behaviour is seasonally highly variable.

2.2 | Data collection

GPS tracking collars of two types (Lotek, Havelock North, New Zealand; and Telemetry Solutions, Concord, USA) were fitted on all LGDs between July 2017 and March 2018, the two types being interspersed across properties. One collar failed at Heatherlie and could not be replaced due to the dog's shyness. Collars took a location every 30 min and were fitted a minimum of 4 weeks before collection of data on foxes. Only locations with a HDOP (horizontal dilution of precision) <10 (Lotek collars) or <4 (Telemetry Solution collars) were retained for analysis. HDOP values were chosen as those that offered the best balance between filtering out inaccurate locations and data retention, based on a pilot study of stationary GPS collars. A mean (±SE) of 3.0% ± 0.4% locations was deleted from the data sets collected by the Lotek collars, resulting in a mean (±SE) HDOP of 2.0 ± 0.05 of the retained sample of locations. A mean (±SE) of 2.4% ± 0.8% was deleted from the data sets collected by the Telemetry Solution collars, resulting in a mean (±SE) HDOP of 1.2 ± 0.09 in the retained sample.

Forty-eight Reconyx PC800 HyperFire Professional IR cameras (Reconyx, Holmen, WI, USA) were distributed over each pair of trial and control properties for a 6-week survey (2016 trap nights). Cameras were set to take three images in rapid succession when triggered, with a minimum 1-minute delay between consecutive triggers to reduce repeat triggers by the same individual. On Riversdale and Wagonbark, this survey ran in August and September 2017; on Heatherlie and Mullameah, it ran in December 2017 and January 2018. Half of the 48 cameras were allocated to the control site and were evenly distributed over the chosen area in a grid pattern. The remaining 24 cameras were distributed over each trial site, according to the intensity of use of different areas by the Maremmas (see below).

A minimum of 4 weeks of data from the GPS-tracking collars were used to calculate a fixed kernel home range (Worton, 1989) for each dog group by pooling the locations of all members. 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 (Jacques et al., 2009; Kie et al., 2010). The package 'adehabitat HR' (version 0.4.19) in R statistical software (Calenge, 2006; R Core Team, 2013) was used for all home range calculations. The 10%, 50%, 90% and 95% isopleths were extracted from this home range calculation, and the area covered by each incremental isopleth was determined. The 24 cameras were distributed in order to equalise camera density for each incremental area, with a higher density in the 10% and 50% isopleth areas to maintain a minimum of two cameras per isopleth zone.

The feeding trials exploited the propensity of foxes to dig for food items and were designed to yield a measurement equivalent to a giving-up density (GUD) that would indicate variation in the willingness of foxes to remain at a site to continue gathering food as a function of the level of risk associated with that site. At each site, we dug a 30-cm deep hole approximately 2 m in front of the camera and filled it in while placing a chicken neck at each 5-cm depth interval, the top chicken neck being buried just below the surface. Chicken necks were chosen based on a pilot study that showed they are favoured by wild foxes. The cameras monitoring the foraging behaviour of foxes at trial sites were set to take three images in rapid succession at each trigger, with no delay between consecutive triggers.

This assay mimics classical GUD experiments because the time required for a fox to obtain each consecutive food item increased with depth (Figure 1). This means that as a fox remains at a site to dig out more food, it experiences a declining rate of food recovery. In addition, shallow food items can be obtained by a fox while still scanning the area for danger, but deeper food items required it to have its head and upper body inside the hole while digging, increasing its vulnerability to attack. As a result, the ratio of risk to reward from continued foraging at the site increases. At sites where foxes

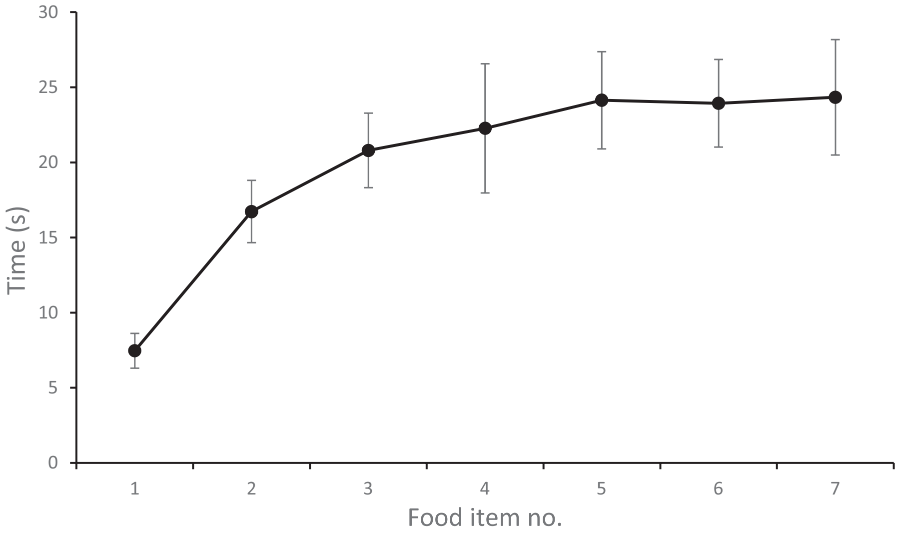

FIGURE 1 The time required to obtain each chicken neck in the fox GUP experiment. Seven chicken necks were buried in a column, with 5 cm between each chicken neck. Chicken neck no. 1 sits just below the surface, no. 7 sits at 30 cm deep. The time on the *y*-axis represents the additional time required by a fox to obtain each consecutive chicken neck. These data were obtained from a pilot study (*N* = 15). Values represent mean ± SE.

perceive higher risk, they should therefore leave more food items unrecovered. We hypothesised that risk was related to the local activity of Maremmas, which in turn varied according to the position of each feeding site in the group range of Maremmas on each property.

2.3 | Data analysis

Two measures of Maremma presence were calculated for each camera site. The first was the probability of Maremma occurrence based on home range calculations. We obtained this probability from a long-term (8-month) home range calculation of each dog group on each property using the Brownian bridge approach of the kernel method (Bullard, 1991; Horne et al., 2007). Locations at the control sites were allocated a value of zero. To enable statistical analysis with these values, they were transformed with the following formula: (log10(probability value + 1))*10,000.

The second measure was the number of days on which Maremmas were detected at each camera site during the survey. As Maremmas were rarely detected on camera (*N* = 9), we identified all instances in which a GPS collar from a Maremma logged a location within 30 m of a camera, and added these to the camera detection data (*N* = 76) to calculate 'days of Maremma detection'. This measure proved to have a greater effect in all models used in our analysis than 'probability of Maremma occurrence', so only 'days of Maremma detection' was used as an indicator of Maremma presence. At Mullameah, all camera locations that fell within 300 m of the wild dog exclusion fence were excluded because of poison baiting along the fence just prior to the research. At Riversdale and Heatherlie, all camera locations beyond the 95% isopleth (obtained from the 8-month home range calculation) were excluded due to continuing lethal fox control on the edge and outside the experimental properties.

In each analysis, all competing models were ranked according to their AIC value (AICc for the foraging experiment; Burnham & Anderson, 2002), and we considered all models that fell within 2 ΔAIC of the top model to be reasonable descriptors of the data.

2.3.1 | Distribution of fox activity

We used single-season occupancy models (MacKenzie et al., 2006) implemented in PRESENCE 2.13.12 (Hines, 2006) to model the distribution of foxes (409 detections in total across all properties). Occurrence matrices were based on 24-h periods, starting at 18:00. We limited our analyses to the probability of detection only, as the cameras were not sufficiently far apart to ensure spatial independence, as required for estimation of occupancy (MacKenzie et al., 2006).

One-species occupancy models determined whether the probability of detection of foxes was influenced by Maremma presence. The covariate 'season/property' was included in all models to account for differences among properties in fox management and time of year. A base model containing only this covariate was compared to the base model plus days of Maremma detection. We used two-species models (MacKenzie et al., 2004, 2006) to test the effect of the presence of Maremmas on the probability of the detection of the foxes. Maremma occurrence matrices included Maremma detections on cameras and Maremma presence within 30 m of the camera sites as logged by the GPS collars. Only the two Maremma properties were included in this analysis, as Maremmas were absent from the control sites.

In PRESENCE, three alternative parameterisations are available for two-species modelling; we used the simplest (MacKenzie et al., 2006). As our analyses were limited to the probability of detection, PsiA and PsiB were modelled independently and Phi was not estimated

(Lazenby & Dickman, 2013; MacKenzie et al., 2006). The parameters that were estimated were: pA, the probability of detecting species A, given that species B is not present; pB, the probability of detecting species B, given that species A is not present; rA, the probability of detecting species A, given that both species are present; rB, the probability of detecting species B, given that both species are present; Delta, species co-detection, which is an expression of whether two species are detected independently at the survey sites. Values <1 indicate that a camera is less likely to detect a species during a 24-h survey period if the other species was detected in that period (suggesting temporal avoidance or exclusion). Values >1 indicate that a camera is more likely to detect a species during a 24-h survey period if the other species was detected in that period (suggesting temporal attraction).

All models included 'season/property' as a covariate. Other covariates were also included in the models to maximise the capture of variation in the data. Two other covariates were considered a priori to potentially influence the probability of the detection of foxes; distance to nearest cover (m), where cover was defined as vegetation that could offer shelter to a fox, such as forest or a patch of large tussocks or bushes and livestock type (sheep, cattle, sheep and cattle, no livestock). For Maremmas, only 'livestock type' was considered to potentially influence their probability of detection. Due to low sample size for the two-species models, 'livestock type' was reduced to 'cattle present' for foxes, and 'sheep present' for Maremmas, to enable model computation. These livestock categories had the highest influence on each species.

A base model containing only the covariate 'season/property' for foxes and Maremmas was ranked with the models consisting of the 'base model' with one additional covariate added for one of the two species at a time; all models containing a covariate ranked higher than the base model. Therefore, multicovariate models were created that consisted of the base model with all combinations of the additional covariates, and these were ranked with the other models. To further explore the effect of Maremmas on foxes, three additional constraints were placed on the models that fell within 2 ΔAIC of the top model: (1) pA = rA, (2) pB = rB and (3) delta = 1 (Lazenby & Dickman, 2013).

2.3.2 | Risk-sensitive foraging by foxes

We recorded the number of food items taken at each camera site and reviewed the images obtained by the cameras. If the cameras showed another species had dug at the site, or if no foxes were detected during the experiment, that site was excluded from analysis. This left 13 sites at Riversdale, 14 at Wagonbark, 15 at Heatherlie and 11 at Mullameah for analysis.

The number of food items taken was added as the dependent variable in a generalised linear model with a Poisson distribution. The covariates from the analysis of fox detection were considered a priori to potentially influence fox behaviour, except that 'days of Maremma detection' was defined as the number of days Maremmas were detected at each camera site during the feeding trial only. 'Season/property' was a random variable in all models. A base model containing only 'season/property' was ranked with the models consisting of the 'base model' with one of the other explanatory variables added at a time. All models containing an additional explanatory variable ranked higher than the base model, so two additional models were created and ranked with the other models. These models contained the following explanatory variables: (a) base model with 'distance to cover' and 'livestock type', (b) model (a) with 'days of Maremma detection'. Analysis used the package 'GLMMadaptive' (version 0.8–5) in R statistical software (R Core Team, 2013).

3 | RESULTS

3.1 | Distribution of fox activity

The top-ranking one-species model for the probability of detecting foxes contained the covariate 'days of Maremma detection' (Table 1). The probability of detecting foxes at a camera location decreased with an increasing number of days that Maremmas had been detected (Figure 2).

TABLE 1 Distribution of fox activity models.

Model covariates	AIC	Delta AIC	AIC weight	No. par
One-species models				
Md	2398.91	0.00	0.74	4
BM	2403.19	4.28	0.09	3
Two-species models				
pM(P), pF(P, cP, dC), rM(p), rF(P, cP, dC)	1904.66	0.00	0.64	11
pM(P, sP), pF(P, cP, dC), rM(P, sP), rF(P, cP dC)	1906.25	1.59	0.29	12
pM = rM(P), pF(P, cP, dC), rF(P, cP, dC)	1910.55	5.89	0.03	10

One-species models: 'Md'; days of Maremma detection, 'BM' (base model) assumes a constant probability of detection for all cameras for each study/control property combination.

Two-species models: The highest ranking models (all models within 2 ΔAIC of the top model), and the nearest contender. Covariates are indicated with the variable they affect. 'M'—Maremma, 'F'—fox, 'p', the detection probability of the species if the other species is not present; 'r', the detection probability of the species if both species occur at the site. The covariates are 'P', season/property; 'cP', cattle presence; 'sP', sheep presence and 'dC', distance to cover.

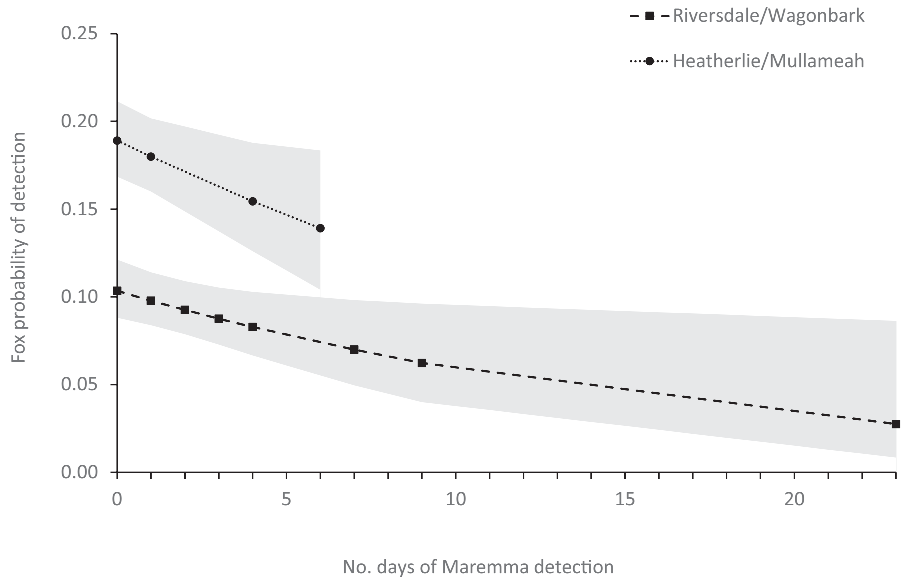

FIGURE 2 The probability of detecting foxes in relation to Maremma detections, as estimated from the one-species models. The shaded area represents the 95% confidence interval of the estimated effect line.

Among two-species models, two top models fell within 2 AIC units of each other (Table 1). In both, foxes were detected less often at camera sites if Maremmas had been detected (Figure 3), and Maremmas were detected more often at camera sites if foxes had been detected at the site. The probability of detecting both Maremmas and foxes at the same site within a 24-h period was less than the probability of detecting either species alone; Delta was 0.62 in both models. Apart from 'property/season', the variables 'distance to cover' and 'cattle presence' were important covariates accounting for the detection of foxes in both top models: Foxes were less likely to be detected on Riversdale, further from cover, and if cattle were present (Figure 3). For Maremmas, 'property/season' was an important covariate included in both top models: Maremmas were less likely to be detected on Heatherlie. 'Sheep presence' was included as a covariate for Maremmas in the second-best model: Maremmas were more likely to be detected in areas with sheep.

3.2 | Risk-sensitive foraging by foxes

The top model included 'days of Maremma detection', 'distance to cover' and 'livestock type' as explanatory variables in addition to 'property' as a random variable (Table 2). The top model was more than six AICc units removed from the next best model and was therefore considered the best descriptor of the data. Fewer food items were taken at sites with more Maremma detections; the pattern shows that where Maremma detections were high foxes always took few or no food items, but that they often took large numbers of items when Maremma detections were low (Figure 4). More food items were taken at Heatherlie/Mullameah, if the site was closer to cover (Figure 4), and with sheep, followed by no livestock, cattle and both sheep and cattle.

4 | DISCUSSION

Interference competition is common between species of mammalian predators and can involve larger predators killing smaller ones (Ritchie & Johnson, 2009). Therefore, mesopredators typically fear larger predators, so modify their behaviour and habitat use to reduce their risk of encountering them (Garvey et al., 2015; Gaynor et al., 2019; Haswell et al., 2018; Switalski, 2003). Our results suggest that foxes responded to LGDs with similar behaviours to those that mesopredators use to avoid encounters with top predators in natural systems.

One of those behaviours was spatial avoidance: Foxes were less likely to be detected in places that were more regularly used by LGDs. However, avoidance was incomplete, and foxes still overlapped with LGDs in our study areas. Our foraging experiment suggests that when foxes did enter areas frequented by LGDs, they were less willing to remain at feeding stations to recover buried food items. The reduced allocation of time to foraging indicates that foxes' feeding behaviour was suppressed in areas where the risk of encountering LGDs was high.

Reduced foraging behaviour by foxes has been observed in response to the presence of wolves, dingoes and lynx *Lynx lynx* (Burgos et al., 2022; Haswell et al., 2018; Leo et al., 2015; Mukherjee et al., 2009). Similarly, cheetahs are less likely to initiate hunts in the presence of lions *Panthera leo* or hyenas *Crocuta crocuta* (Cooper et al., 2007; Durant, 2000). This response could be because mesopredators need to be vigilant when in areas of high activity of top predators. Given the results of our experiment on risk-sensitive foraging, it is likely that the foxes in our study also spend less time hunting in areas where LGDs were present, reducing predation risk for both livestock and wildlife. This is because maintaining vigilance against larger predators disrupts hunting and also increases the time needed to complete

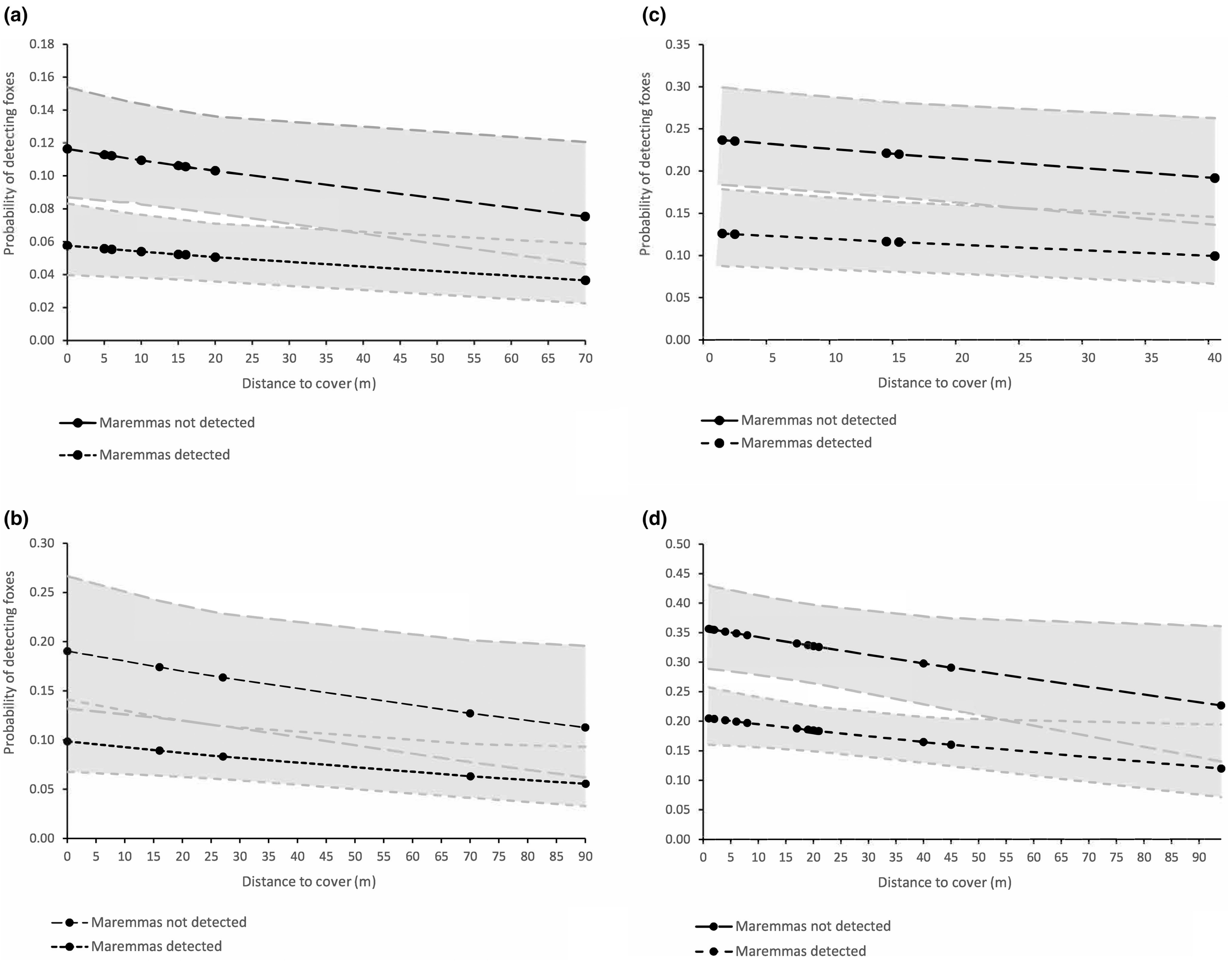

FIGURE 3 Fox detection probabilities in the presence and absence of the detection of Maremmas at the experimental sites, as estimated from the two-species models. Distance to cover and the presence of cattle were important covariates in the model. The shaded area represents the 95% confidence interval of the estimated effect line. (a) Riversdale, cattle present, (b) Riversdale, cattle not present, (c) Heatherlie, cattle present, (d) Heatherlie, cattle not present.

complex sequences of hunting behaviour (MacNulty et al., 2007). For these reasons, hunting in areas with high presence of larger predators is not only risky but also inefficient, so mesopredators shift their hunting activity to other areas.

Our results have implications for the use of LGDs both in livestock protection and biodiversity conservation. Previous research suggests that LGDs could protect livestock either by keeping predators out of the areas they occupy, and therefore away from livestock (McGrew & Blakesley, 1982; van Bommel & Johnson, 2014a), or by remaining close to their livestock to ward off attacks by predators who remain in the area (Coppinger & Schneider, 1995; McGrew & Blakesley, 1982). In our study areas, foxes were not excluded from areas occupied by LGDs. However, the negative relationship of detection of foxes to detection of LGDs suggests that complete exclusion might be possible at high LGD density. We worked on large farms where wide-ranging LGDs were deployed at low density. Under these conditions, foxes were able to continue to use all areas of the farms. Nonetheless, LGDs prevented losses of sheep on the two farms that used them (A. Bowran and J. Fraser, pers. comm), making it clear that exclusion of predators is not necessary for protection.

LGDs certainly do directly repel predators that attempt to attack livestock, to the point of counter-attacking if necessary and sometimes killing the offenders (Hansen & Smith, 1999; Landry et al., 2020; McGrew & Blakesley, 1982). Our results show that LGDs can also change predator behaviour, causing them to be less likely to engage in foraging behaviour in areas where LGDs are present. This could translate into suppression of hunting behaviour of predators, who are then therefore less likely to initiate attacks on prey in places with high activity of LGDs. The foxes in our study did not reduce their feeding because they were interrupted by LGDs; all instances of foxes interacting with feeding stations were monitored and in no case was the departure of a

TABLE 2 Explanatory variables included in the models for the analysis of the number of food items taken in fox GUP experiment.

Model covariates	AICc	Delta AICc	AICc weight
Md**, dC**, Lt	224.96	0.00	0.85
Md**	229.68	6.55	0.03
dC**, Lt	235.92	12.79	0.00
dC*	243.19	20.06	0.00
Lt	244.97	21.84	0.00
BM	247.53	24.40	0.00

Note: 'Md', days of Maremma detection; 'dC', distance to cover; 'Lt', livestock type. 'Season/property' was always included as a random explanatory variable.

$^{*}p < 0.05$; $^{**}p < 0.01$.

fox due to arrival or approach of an LGD. Rather, foxes apparently modified their own behaviour, presumably using cues such as scents and sounds that indicate risk of encountering an LGD and making foraging decision based on the landscape of fear established by the LGDs.

LGDs tend to range widely, and they advertise their presence by frequent scent-marking and barking, so they can indirectly influence predator behaviour over areas that extend beyond the regular limits of movement of their livestock. The preventative effect of this would greatly add to the protection that LGDs provide for the animals in their care. It would also help alleviate the stress that would otherwise be placed on livestock by predation attempts (van Bommel, 2010). Approaches by predators are acutely stressful events for livestock, and repeated experience of them can induce a

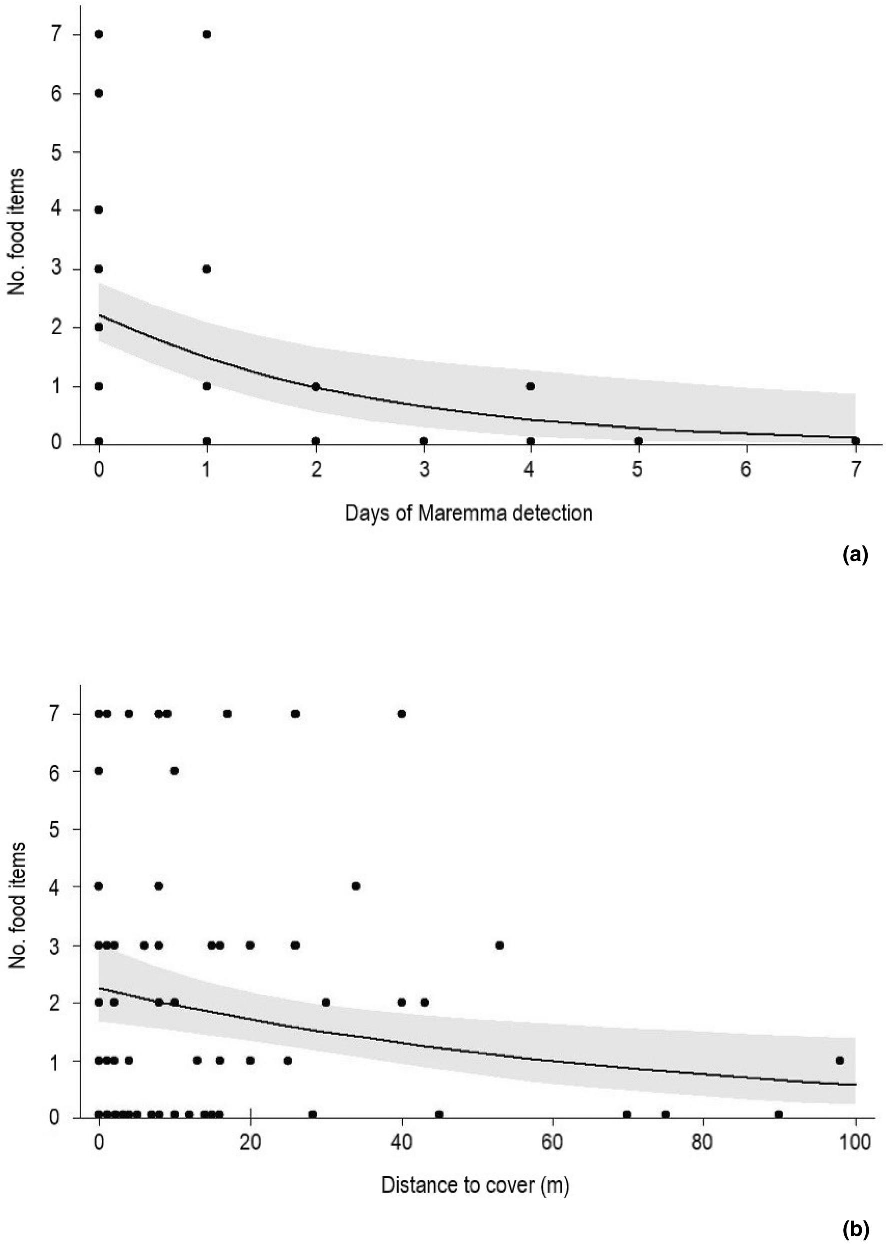

FIGURE 4 Effects of the covariates in the models used in the analysis of the number of food items taken during the fox giving-up density experiment. (a) The effect of the number of days during the experiment that Maremma was detected at each site on the number of food items taken by foxes. (b) The effect of the distance to cover on the number of food items taken by foxes. The shaded area represents the 95% confidence interval of the estimated effect line, and the black dots are the measurements from the experiment.

state of chronic stress (Clinchy et al., 2013; Dwyer & Bornett, 2004). This in turn can cause long-lasting harms to health and welfare, and reduce production (Dwyer & Bornett, 2004).

LGDs can contribute to biodiversity conservation in two main ways. First, by reducing conflict with livestock producers, they reduce or prevent retaliatory killing of predators by farmers, which is a significant threat to large predators worldwide (Kruuk, 2003; Macdonald et al., 2013). Farmers who use LGDs are likely to reduce or cease lethal control of wild predators (González et al., 2012; Potgieter et al., 2016; van Bommel & Johnson, 2023), removing an important source of mortality in predator populations. However, the net benefit of LGDs for predator populations also depends on their effects on predator distribution: If LGDs exclude predators from large areas of habitat, this could reduce their access to important resources and so limit their abundance. Our results suggest that large-scale coexistence of LGDs and wild mesopredators is possible because of fine-scaled adjustments in the behaviour of predators. These results are consistent with the research from Spencer et al. (2020), who showed that predators remain present on farms with LGDs in South Africa.

Second, LGDs might support the conservation of some species of wildlife that are threatened by wild predators, and which could therefore benefit from lower intensities of predation in areas with high activity of LGDs. This effect could be most significant for small-bodied species that use the same habitats as livestock and which are cryptic or unaffected by LGDs, but vulnerable to predators that are influenced by LGDs. Gehring et al. (2010) found that fields with LGDs had more ground-nesting birds than fields without LGDs, which they interpreted as a response to suppression of mesopredators. The red fox in Australia is an invasive species that threatens many small mammals, reptiles and ground-dwelling birds that could otherwise live in habitats grazed by sheep and cattle. LGDs associated with livestock could provide those prey species with indirect protection.

This study shows that LGDs imposed a strong spatial pattern on the fine-scale distribution of fox activity and foraging behaviour, similar to a landscape of fear imposed by large wild predators. The benefits of this for livestock production and biodiversity conservation are potentially complementary and could help restore biodiversity on farming properties. Reduced attacks on livestock could lead to reduced stress in stock, improving animal welfare, productivity, and the viability of farm businesses. LGDs can also give peace of mind to farmers who know that predator attacks on livestock are unlikely to occur if guardian dogs are present, and thereby reduce farmers' stress levels (Gehring et al., 2010; van Bommel, 2010). If livestock are protected, livestock owners are less likely to kill predators, benefitting survival of predator populations. In addition, small prey species could find refuge from predation in LGD ranges, which can greatly benefit biodiversity conservation on grazing properties.

AUTHOR CONTRIBUTIONS

Linda van Bommel, Chris N. Johnson, Michael Magrath and Graeme Coulson conceived the ideas and designed methodology; Linda van Bommel collected the data; Linda van Bommel analysed the data; Linda van Bommel and Chris N. Johnson led the writing of the manuscript. All authors contributed critically to drafts and gave final approval for publication. Our study was an applied research project, based on local data collection and analysis of primary data. The authorship team represents the region of interest.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest in publishing this work.

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Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.z08kprrkr (van Bommel et al., 2023).

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