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Original Research

A Livestock Guardian Dog by Any Other Name: Similar Response to Wolves Across Livestock Guardian Dog Breeds☆

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ABSTRACT

Nonlethal tools for reducing livestock depredations, such as livestock guardian dogs (LGDs; *Canis familiaris*), reduce lethal management of livestock predators and have been widely adopted by domestic sheep *(Ovis aries)* producers in the United States. However, compared with their success in reducing coyote *(Canis latrans)* depredations, commonly used LGD breeds appear less effective against wolves *(Canis lupus).* With more than 30 distinct LGD breeds found throughout the world, certain breeds may be more effective at deterring specific threats. We compared LGD breeds commonly used in the United States, collectively called whitedogs, with three European breeds selected for boldness toward carnivores, history of use in areas with wolves, lack of aggression toward humans, and size. We collected data on LGD behavior with sheep herds in Idaho, Montana, Oregon, Washington, and Wyoming in 2015 and 2016. We also developed a test to examine LGDs' response to a simulated encounter with a wolf while on summer grazing range. Results from generalized linear mixed models of proportion of time spent in a given behavior indicate that few significant behavioral differences exist among tested breeds. Kangals tended to be more investigative when engaging a decoy, karakachans more vigilant, and transmontanos more able to decipher a threatening from unthreatening stimulus. Transmontanos also spent less time scanning than whitedogs, and there was a marginally significant effect of karakachans moving more than whitedogs. While these subtle behavioral differences may help livestock producers make tailored decisions in choosing the appropriate LGD for their needs and circumstance, our results suggest that behavioral differences among breeds may be less common than often suggested.

Introduction

Livestock guardian dogs (*Canis familiaris;* LGDs), also referred to as livestock protection dogs, have been used by humans to mitigate depredation of livestock for at least 5 000 yr (Gehring et al., 2010). Contemporary research on LGDs indicates they are effective for reducing livestock loss (Green et al., 1984; Andelt, 1992; Andelt and Hopper, 2000; van Bommel and Johnson, 2012), although actual loss prevention varies from 11% to 100% (Smith et al., 2000). More than 30 distinct LGD breeds are found throughout the world, most of them endemic to only a single country or region (Rigg, 2001). Likely the result of geographic isolation and selective breeding to meet the needs of local pastoralists, each breed adapted according to different circumstances and demands (Coppinger and Coppinger, 2002; Rigg, 2001). This diversity has led some to speculate as to whether certain breeds may be more effective at deterring specific threats (Urbigkit and Urbigkit, 2010).

Despite generations of use in Europe and Asia, the use of LGDs in other parts of the world is relatively new. In the United States, LGDs gained popularity as a nonlethal alternative to poison for predator control and began to be imported in the late-1970s (Gehring et al., 2010). The Great Pyrenees is the most popular breed in the United States, along with the Akbash, Maremma, Anatolian shepherd, and Komondor (Green and Woodruff, 1980; Green et al., 1984; Andelt and Hopper, 2000), although many working LGDs are genetic crosses of these and other breeds. Although mongrel dogs have been successfully used by the Navajo tribes of the southwestern United States as livestock guardians (Black and Green, 1985; Coppinger et al., 1985), there is no LGD breed endemic to North America.

Following the reintroduction of wolves *(Canis lupus)* to the Western United States, there has been renewed interest in the relative effectiveness of LGD breeds among domestic sheep *(Ovis aries)* producers. LGD breeds initially selected for use in the United States were selected to reduce depredations by coyotes *(Canis latrans)* at a time when wolves were almost entirely absent from the landscape (Bangs et al., 2005). LGD breeds and crosses currently used in the United States may not

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be well suited to dealing with large carnivores because deterring different predators requires different responses (Coppinger et al., 1988). However, there are LGD breeds in Europe and Asia that are currently underused in the United States, and many of them have long histories of deterring wolves in their native countries (Rigg, 2001). Variations in behavior between these European LGD breeds and LGDs bred in the United States may account for the differences in predator-specific effectiveness.

Minimizing depredation of livestock is the obvious goal of LGDs, but it is also important to understand the behavioral mechanisms that mediate their effectiveness. There were limited attempts to compare LGD breed effectiveness shortly after their use in the United States began, but findings were largely inconclusive (Green and Woodruff, 1983, 1988). A recent behavioral investigation of LGDs in Australia focused on their space-use and activity patterns as measures of effectiveness (van Bommel and Johnson, 2014a, 2014b). For instance, van Bommel and Johnson (2014b) showed that maremma sheepdogs outfitted with Global Positioning System (GPS) collars exhibited primarily crepuscular activity patterns, as well as lower levels of activity throughout the night, roughly corresponding to the activity patterns of predators in the area. Although van Bommel and Johnson (2014a) also documented the response of maremma sheepdogs to simulated dingo incursions into a sheep pasture, this recent investigation is limited in scale because it only examined the maremma sheepdog breed of LGD.

Here we examine the behavior of three European LGD breeds not commonly used in the United States and compare behavior to a number of domestically bred LGD crosses. To identify LGD behavior salient to guarding, we partnered with US sheep producers working in wolf-occupied areas to quantify baseline LGD behavior, as well as LGD response to a wolf encounter. Ethical and practical considerations preclude staging interactions of LGDs with wolves, so we developed a test to simulate a wolf encounter while LGDs were on grazing allotments. We analyzed all data with the intent to identify any behavioral differences that exist between LGD breeds, which could affect their ability to guard against large predators.

Methods

Livestock Guardian Dog Breeds

We imported three novel-breed LGDs from August 2012 to October 2016 and placed them with participating sheep producers in Idaho, Montana, Oregon, Washington, and Wyoming. Breeds include the Turkish kangal, the Bulgarian karakachan, and the Portuguese cão de gado transmontano (henceforth “transmontano,” Fig. 1). Breeds were selected for their boldness toward large carnivores, history of use in areas with wolves, lack of aggression toward humans, and larger average size (Rigg, 2001; Urbigkit and Urbigkit, 2010). We imported most LGDs from their countries of origin, but some kangals were sourced in the United States from reputable breeders who were able to trace the purebred status to their Turkish origins. Novel-breed LGDs were placed with participating producers immediately after their arrival, at which time they were cared for by the producers and their staff and bonded to their sheep using traditional practices (Dawydiak and Sims, 2004). All novel-breed LGDs were spayed and neutered at about 1 yr of age to minimize problems of unintentional breeding and wandering. We also monitored extant LGDs, already belonging to some of our participating producers. These “whitedogs” include crosses of multiple LGD breeds and LGDs of unknown genetic origin (see Fig. 1). For the purpose of comparison, we treated them as a single control breed. LGDs worked

Figure 1. Livestock guardian dog breeds tested during this study. Clockwise from bottom left: Portuguese cão de gado transmontano, Bulgarian karakachan, Turkish kangal, American “whitedog.”

in teams of three dogs of the same breed per flock of sheep during the summer grazing season whenever possible. However, due to the constraints of working with working livestock ranches, we accounted for deviations from this study design at the time of analysis by including crossed random effects of individual LGD and trial.

Study Area

We collected data from May to October in 2015 and 2016. Study sites included parts of Wenatchee National Forest and lowland sections of Eastern Washington; the Blue Mountains in Oregon; the western edge of Payette National Forest and the southern edge of Sawtooth National Forest in Idaho, from McCall to Ketchum; the front range in Montana, from Shelby to Dillon; and Bighorn National Forest in Wyoming (Fig. 2). Because of the large geographic distribution of study sites, habitat characteristics varied. Sites were selected for the presence of domestic sheep on summer grazing pastures and the potential for depredation by wolves. This included remote areas of public lands where livestock are grazed by permit through the Forest Service or Bureau of Land Management, as well as fenced and unfenced private lands. In many of these locations there is a history of conflict between sheep producers and large carnivores, while others were deemed to have the potential for conflict due to proximity to extant populations of wolves. We based such designations on input from state and federal wildlife officials and area livestock producers. All behavioral observations were done between 600 and 3 000 m in elevation (most between 1 200 m and 1 400 m) and ≤ 500 m from a grazing sheep band, during daylight hours between 06:00 and 23:00.

Baseline Behavior

To develop a baseline of typical LGD behavior by breed, dogs were observed and their behavior was recorded up to once a week over two field seasons using continuous focal sampling techniques (Altmann, 1974; Martin and Bateson, 2007). Generally, a single observer recorded continuous focal sampling after at least a week of training with a graduate student and coworkers. However, we collected observations in teams three to four times per month, with the graduate student assisting technicians to increase consistency and reduce interobserver error. To maximize the amount of data collected, we recorded each behavioral observation as a four-component code: 1) activity, 2) posture, 3) vocalization, and 4) proximity-to-sheep (Table 1). Each time an LGD changed states in any of the four components, an observer would record the time of the state change and a four-character code corresponding to the new behavioral state. At the time of analyses, we analyzed these four components of behavior separately. We observed 80 individual LGDs of four different breeds (kangal = 19, karakachan = 12, transmontano = 12, whitedog = 37), in a repeated measures design (kangal = 207, karakachan = 87, transmontano = 82, whitedog = 164). Observations lasted 20 min per LGD but were occasionally shorter due to LGDs moving out of view. A total of 170 hr of observations were recorded across 540 trials. However, in three of the 540 trials, LGDs

Table 1
Behavioral codes used during continuous focal observations and the decoy test. Behavior is divided into four components, and one behavior from each component was recorded at every observation. Note that the "decoy" behavior under proximity was only an option during the decoy test.

Behavioral component	Behavior	Description
Activity		
	Vigilant	Attention fixed
	Investigate	Sniffing an area or object
	Scan	Looking around or scanning an area
	Run	Running after another animal
	Stalk	Head, tail, and ears lowered; crouched pursuit
	Chase	Running after another animal
	Fight	Fighting with, or biting another animal
	Play	Playing with other dogs
	Eat	Eating or drinking
	Hygiene	Grooming, urinating, defecating
	No behavior	No behavior observed
Posture		
	Lay	Lying or bedded-down (includes sleeping)
	Up	Sitting or standing stationary
	Move	Moving, any speed
Vocalization		
	Bark	Barking
	Growl	Growling
	Whine	Whining
	No sound	No audible sound
Proximity		
	Sheep	≤ 50 m from sheep
	Away	> 50 m from sheep (and decoy)
	Decoy	≤ 50 m from decoy (only during decoy test)
Other		
	Out-of-view	Not visible to the observer

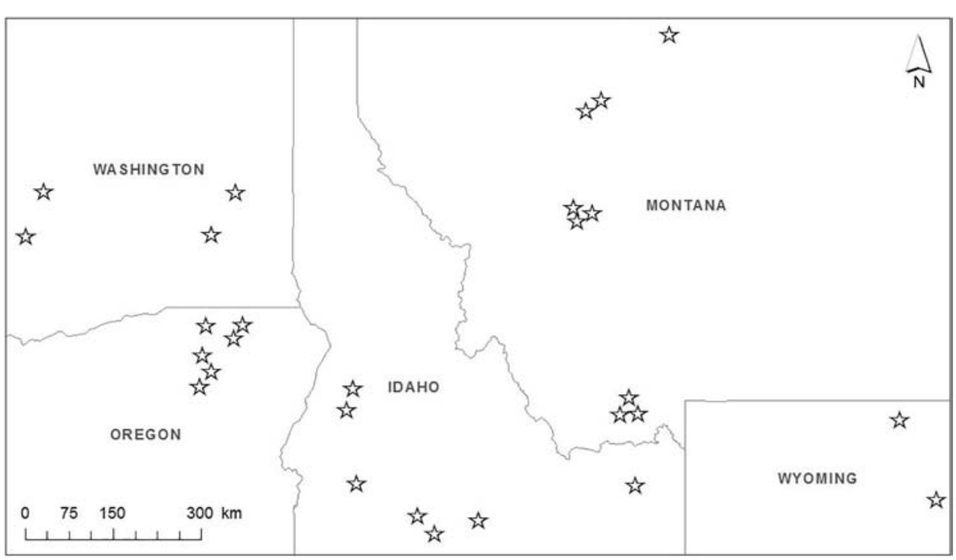

Figure 2. Study extent. *Stars* indicate the locations of monitored LGDs and sheep bands from 2015 to 2016.

went out of view of the observers immediately after the test began and never came back into view. For an additional 27 trials, information on a whitedog's age or sex was unavailable, either because the whitedog could not be identified at the time of the test or because detailed records were not available for extant whitedogs. These trials were withheld from analysis, resulting in a sample size of 509 trials (Fig. 3).

Decoy Test

Although an important component of LGD effectiveness is how the animals respond during encounters with livestock predators, these encounters are infrequent and difficult to observe. Instead, we simulated an encounter between LGDs and a wolf using a decoy and recorded the behavioral response. We constructed two decoys for the test to measure LGD response to a threatening wolf decoy and a nonthreatening deer decoy. Decoys were constructed in the field using a premeasured polyvinyl chloride frame skeleton. A mule deer *(Odocoileus hemionus)* hide was used for the deer decoy, and a wolf hide was used with the wolf decoy. We also paired each decoy with a remote-controlled call device that was programmed to play an elk bugle when paired with the deer decoy and a wolf howl when paired with the wolf decoy. In the field, decoys were constructed within 100–500 m of sheep grazing with LGDs, but out of site of the LGDs. Once the decoy was constructed, observers hid out of sight in a nearby location with a clear view of the decoy and played the call device to alert the LGDs to the presence of the decoy. The call (i.e., howl or bugle, depending on decoy type) was played for 2 min or until the first LGD arrived at the decoy (≤ 20 m), whichever came first.

LGD response was recorded using instantaneous scan sampling (Altmann, 1974; Martin and Bateson, 2007) every 15 sec, for all LGDs

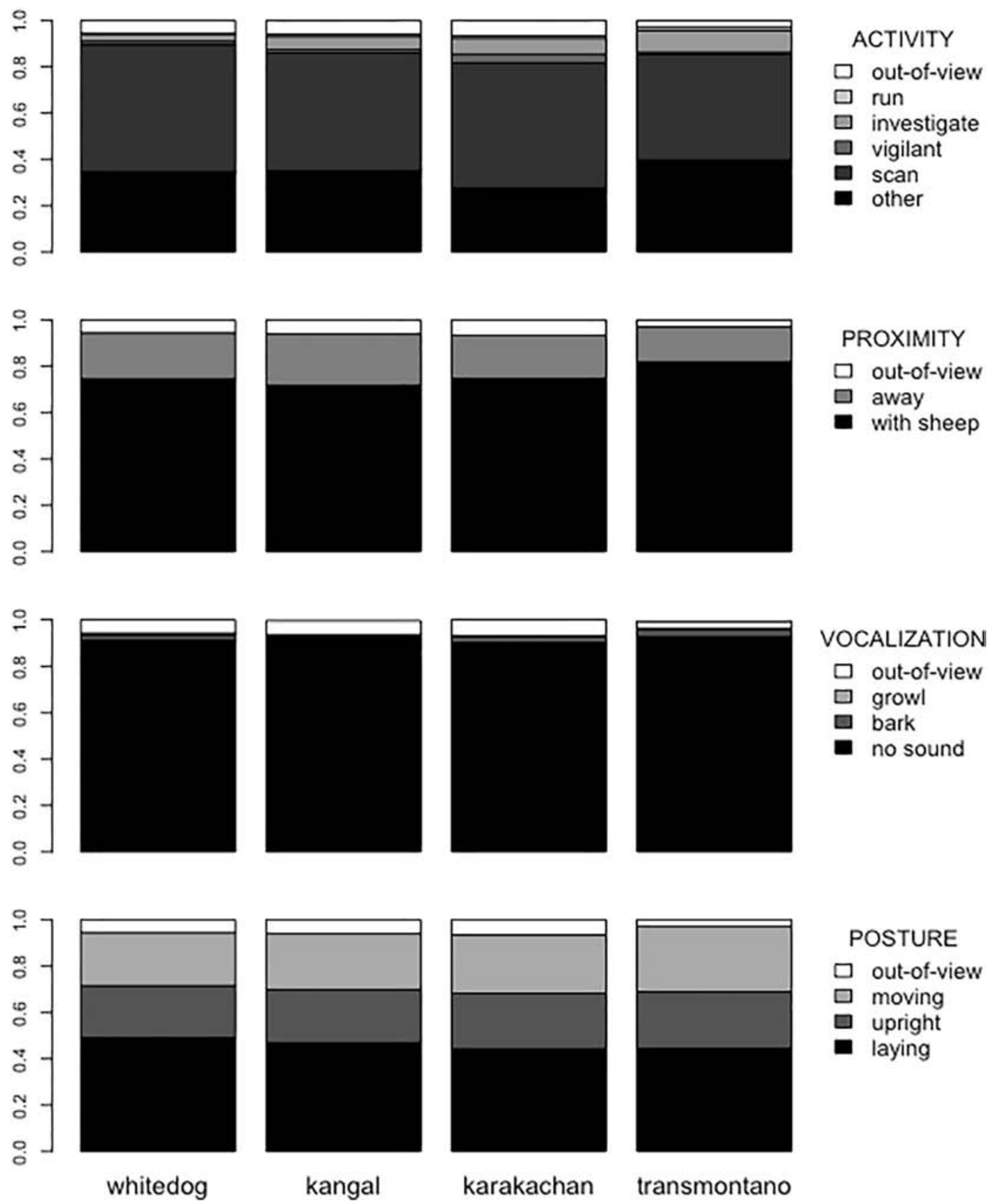

Figure 3. Proportion of time spent in each behavioral state, averaged across 540 tests of 80 individual livestock guardian dogs. The four behavioral components (activity, proximity, vocalization, posture) are shown by row. Proportion of behavior is collapsed by breed (whitedog, kangal, karakachan, transmontano) and shown by column. Play, eat, hygiene, chase, stalk, fight, and no behavior are collapsed into a single "other" category in activity for readability.

in view. At least two researchers were present for every decoy test, with one present for the majority of tests and responsible for all training of research participants, to increase consistency and minimize interobserver error. We observed 84 individual LGDs of four different breeds (kangal = 19, karakachan = 8, transmontano = 9, whitedog = 48), in a repeated measures design (kangal = 57, karakachan = 19, transmontano = 17, whitedog = 118). Decoy tests lasted 5–30 min. We ended tests after 2 continuous min of inactivity or neutral behavior from the LGDs (usually returning to the sheep) with most tests lasting < 10 min. However, some tests lasted much longer and were ended at 30 min by the observer if the LGD never stopped engaging with the decoy. Individual LGDs were tested no more than twice per year (once with the deer decoy and once with the wolf decoy) to avoid habituating LGDs to potentially threatening environmental stimuli like wolf howls. The order in which the decoys were presented to each group of LGDs was randomized with a coin flip before the first test in each grazing year. Behavior was recorded using the same four-character code as in the continuous focal sampling test. A total of 7 772 observations were collected across 214 trials in 64 tests. However, in 87 of the 214 trials LGDs remained out of view of the observers for the entirety of the test. These trials were withheld from analysis. For an additional 27 trials, information on an LGD's age or sex was unavailable. These trials were also withheld from analysis, resulting in a final sample size of 100 trials (Fig. 4).

Statistical Analysis

We focused analyses on behavior believed to be most relevant to guarding effectiveness. This included vigilant, investigate, scan, run, bark, move, lay, and with sheep (Table 1). While behavior like stalk, chase, fight, and growl are also likely to be related to LGD effectiveness, they were observed so rarely that we excluded them from analysis. Unlike the continuous focal observation dataset, which was ended or restarted when an LGD went out of view, it was possible for LGDs to be out of view for large proportions of the decoy test. As such, we included time spent out of view as a unique behavior to determine if time spent out of view was a random artefact of our test protocol or if it varied systematically by one or more of our a priori predictor variables.

The proportion of time LGDs spent in each relevant behavioral state (i.e., vigilant, investigate, scan, run, bark, move, lay, and with sheep) was calculated for each trial and analyzed separately as the response variable of interest in a set of generalized linear mixed-models (GLMMs) with a binomial error structure (Warton and Hui, 2011; Broekhuis et al., 2014). Model sets for each behavior included a random effect of individual LGD to account for repeated measures of dogs across season and across year. To account for overdispersion, we included a random variable of trial for continuous focal observations (i.e., unique for every observation) and a random variable of test for the decoy data set (i.e., all LGDs observed in a single test). As number and composition

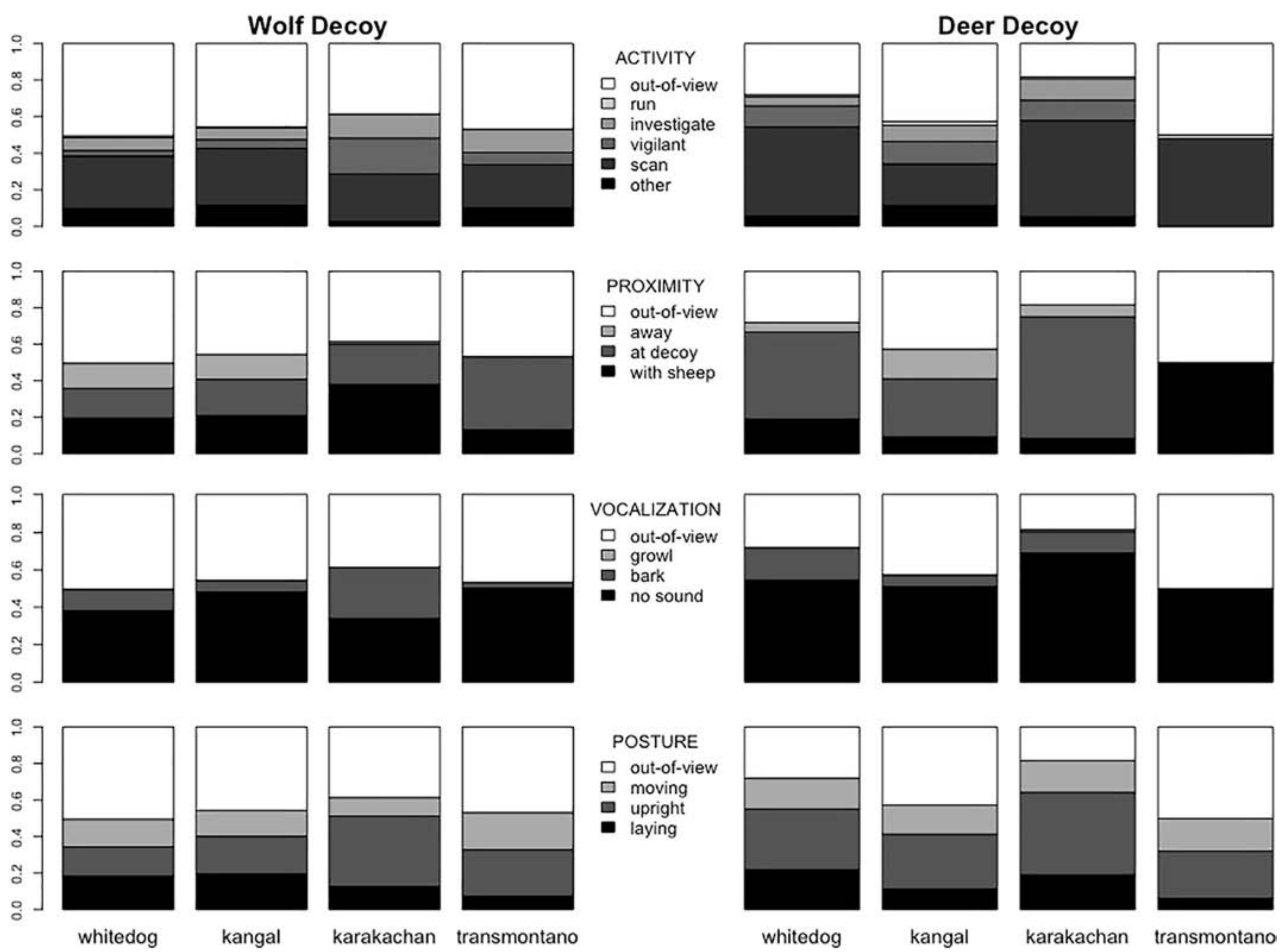

Figure 4. Proportion of time spent in each behavioral state, averaged across 214 tests of 84 individual LGDs. The four behavioral components (activity, proximity, vocalization, posture) are shown by row. Decoy type (wolf, deer) is shown in the two major columns. Proportion of behavior is collapsed by breed (whitedog, kangal, karakachan, transmontano) and shown by subcolumn. Play, eat, hygiene, and no behavior are collapsed into a single "other" category in activity for readability.

of individual LGDs varied by trial, the two random variables were treated as crossed random effects. Categorical predictor variables include LGD breed (kangal, karakachan, transmontano, "whitedog"); LGD sex (male, female); and LGD age category (juveniles < 2 yr old, adults ≥ 2 yr old). For the continuous focal data set we also included a categorical variable for time of day (morning: 07:00–11:59, midday: 12:00–16:59, evening: 17:00–22:00). For the decoy data set we also included as a categorical variable decoy type (wolf, deer). As all combinations of a priori predictor variables were considered to have biological relevance, we treated all combinations of main effects as candidate models for proportion of time spent in each behavioral state. Including interaction terms generally caused models to fail to converge. Due to limited sample size, we did not test for interactions. For the decoy set, in addition to modeling all behavior observed during the test, we also modeled LGD behavior from only the first 60 sec (up to four observations) after an LGD arrived at the decoy. These analyses were performed to determine if breed differences in LGD behavior during the decoy test might only be associated with initial response. Transmontanos had to be removed from this analysis because no transmontano ever engaged the deer decoy.

We also analyzed time-to-approach and time-to-leave for the decoy using a Cox proportional hazards analysis (Kleinbaum and Klein, 2005). Using proximity data from the decoy test, we calculated the time from the beginning of the test to the first time an LGD was ≤ 50 m from the decoy (time-to-approach, $n = 140$) and the time from the first observation during which a LGD was ≤ 50 m from the decoy to the last observation during which a LGD was ≤ 50 m from the decoy (time-to-leave, $n = 43$). As with the behavioral models of decoy data, categorical predictor variables include decoy, LGD breed, LGD sex, and LGD age category. A random effect was included for each individual LGD to account for repeated measures of dog across season and across year. To account for overdispersion, we included a random effect of test. We consider all combinations of these a priori predictor variables to be biologically relevant and therefore included all combinations of main effects as candidate models.

Analyses were run using the statistical software R 3.3.2 (R Core Team, 2016) with the lme4 package (version 1.1–12) for GLMMs (Bates et al., 2015) and the coxme package for Cox proportional hazards models containing random effects (Therneau, 2015). We tested for model convergence using the default bound optimization by quadratic approximation (BOBYQA) optimizer in lme4. We tested for overdispersion using the "overdisp_fun" function in R (available at http://bbolker.github.io/mixedmodels-misc/glmmFAQ.html). All models in each model set were ranked using Akaike Information Criterion for small samples (AICc). We considered all models with a delta AICc ≤ 2.0 top models.

Results

Baseline Behavior

Two of seven top models indicate that transmontanos are about a third as likely to engage in scan behavior compared with whitedogs ($P < 0.04$, Table 2), with the same effect approaching significance in other top models. Additionally, in six of the seven top models of scan behavior, scanning was more than twice as likely to occur in the evening compared with midday ($P < 0.02$, see Table 2). Model sets for the move and lay postures indicate that laying was less common and moving more common in the morning and evening relative to midday ($P < 0.01$) in all top models from each model set (Tables 3 and 4). One of the top models for the move data set (ΔAICc $= 1.71$) indicates an effect of breed approaching significance ($P = 0.054$), which suggests that karakachans may be more likely to exhibit move posture than whitedogs (see Table 3). For the behavior vigilant, investigate, run, with sheep, and bark, the null model was the highest-ranking model and no predictor variables reached a threshold of significance ($P < 0.05$) in any of the other top models. For some of the models using the continuous focal dataset as input, convergence problems were encountered in models that included time of day (see Table S1), but all top models converged successfully except for model 5 of the scan behavior model set (max|grad| $= 0.0036$, tol $= 0.001$; see Table 2).

Decoy Test

Because models of out-of-view with a random effect of test showed significant evidence of overdispersion, we instead included a random effect for each LGD in a given test. The top model for out-of-view was the only model in the set with a delta AICc < 2.0, and it indicates a significant effect of age, with juvenile LGDs 2.7 times as likely to be out of view as their adult counterparts ($P = 0.03$). The only behavior in the decoy test with significant predictors was vigilant, where all three top models indicate that juvenile LGDs were about four times as likely to

Table 2
Model results for all top models (ΔAICc ≤ 2.0) of the scan behavior observed during continuous focal observations. Results are shown as log odds ratios with standard error shown in parentheses below. Any models that failed to converge are indicated.

	Top scan models						
	(1)	(2)	(3)	(4)	(5)	(6)	(7)
Morning vs. midday	0.445	0.413	0.443	0.428	0.394	0.465	
	(0.354)	(0.354)	(0.355)	(0.354)	(0.354)	(0.356)	
Evening vs. midday	0.852**,***	0.848**	0.828**	0.855**	0.853**	0.831**	
	(0.349)	(0.350)	(0.350)	(0.349)	(0.350)	(0.350)	
Kangal vs. whitedog	0.163	0.087		0.033	−0.060		0.142
	(0.422)	(0.432)		(0.447)	(0.454)		(0.422)
Karakachan vs. whitedog	0.746	0.683		0.532	0.435		0.622
	(0.531)	(0.545)		(0.581)	(0.593)		(0.528)
Transmontano vs. whitedog	−1.045*	−0.907*		−1.270**	−1.180*		−1.118**
	(0.540)	(0.548)		(0.592)	(0.604)		(0.539)
Male vs. female	0.605*			0.575		0.369	0.586
	(0.360)			(0.365)		(0.380)	(0.359)
Juveniles vs. adults				0.339	0.398		
				(0.356)	(0.359)		
Model convergence					*Failed*		
log likelihood	−3 308.37	−3 309.73	−3 312.88	−3 307.92	−3 309.11	−3 312.42	−3 311.41
ΔAICc	0.00	0.64	0.79	1.18	1.49	1.91	1.95
Model weight	0.164	0.119	0.111	0.091	0.078	0.063	0.062

* $P < 0.1$.
** $P < 0.05$.
*** $P < 0.01$.

Table 3
Model results for all top models (dAICc < 2.0) of the move behavior observed during continuous focal observations. Results are shown as log odds ratios with standard error shown in parentheses below. Any models that failed to converge are indicated.

	Top move models			
	(1)	(2)	(3)	(4)
Morning vs. midday	1.670*	1.671*	1.705*	1.652*
	(0.482)	(0.482)	(0.483)	(0.483)
Evening vs. midday	1.254*	1.287*	1.358*	1.255*
	(0.478)	(0.479)	(0.482)	(0.478)
Juveniles vs. adults		0.464		
		(0.401)		
Kangal vs. whitedog			0.653	
			(0.492)	
Karakachan vs. whitedog			1.179**,***	
			(0.611)	
transmontano vs. whitedog			0.109	
			(0.633)	
Male vs. female				−0.226
				(0.417)
Model convergence				
log likelihood	−2 604.14	−2 603.47	−2 601.91	−2 603.99
ΔAICc	0.00	0.71	1.71	1.76
Model weight	0.305	0.214	0.130	0.127

* $P < 0.01$.
** $P < 0.1$.
*** $p<0.05$;

be vigilant during the decoy test relative to their adult counterparts ($P < 0.01$, Table 5). For behavior investigate, lay, with sheep, with decoy, bark, and move, the null model was among the highest-ranking models and no predictor variables reached a threshold of significance in any of the other top models (see Table S2). Observations of the run behavior were so infrequent in the decoy test dataset that most models failed to converge (see Table S2).

Modeling only behavior observed in the first 60 seconds after a LGD engaged with the decoy, we observed significant breed differences but no difference between decoy types. Karakachans were approximately 20 times more likely to be observed vigilant than kangals in two of the six top models ($P < 0.05$, Table 6). Kangals were eight times more likely to have been observed investigating than whitedogs ($P < 0.05$, Table 7). Transmontanos had to be removed from the analysis because no transmontano ever engaged the deer decoy. For the behavior scan, run, bark, and move, the null model was among the highest-ranking models and no predictor variables reached a threshold of significance in any of the other top models (see Table S3). Observations of the lay posture were so infrequent in the abbreviated decoy test dataset that we did not analyze the behavior.

Table 4
Model results for all top models (dAICc < 2.0) of the lay behavior observed during continuous focal observations. Results are shown as log odds ratios with standard error shown in parentheses below. Any models that failed to converge are indicated.

	Top lay models	
	(1)	(2)
Morning vs. midday	−1.641*	−1.639*
	(0.573)	(0.573)
Evening vs. midday	−1.460*	−1.472*
	(0.565)	(0.566)
Juveniles vs. adults		−0.208
		(0.4198)
Model convergence		
Log likelihood	−2 831.52	−2 831.43
ΔAICc	0.00	1.87
Model weight	0.428	0.168

*p<0.1; **p<0.05;
***$P < 0.01$.

Table 5
Model results for all top models (dAICc < 2.0) of the vigilant behavior observed during the decoy test. Results are shown as log odds ratios with standard error shown in parentheses below. Any models that failed to converge are indicated.

	Top vigilant models		
	(1)	(2)	(3)
Juveniles vs. adults	1.335*	1.370*	1.380*
	(0.449)	(0.442)	(0.457)
Wolf vs. deer decoy		−0.652	
		(0.623)	
Male vs. female			−0.216
			(0.360)
Model convergence			
Log likelihood	−186.92	−186.39	−186.74
ΔAICc	0.00	1.16	1.85
Model weight	0.409	0.229	0.162

*p<0.1; **p<0.05;
***$P < 0.01$.

Time-to-Approach and Time-to-Leave Decoy

For time-to-approach and time-to-leave decoy, neither top model set included predictor variables that reached significance. A trend was evident in the time-to-approach data of a marginally faster average response to the wolf decoy, but it does not reach statistical significance ($P < 0.05$). A table of all ranked models is included in supplemental material (Table S4; available online at https://doi.org/10.1016/j.rama.2018.03.004).

Discussion

Our study found that kangals, karakachans, transmontanos, and whitedogs spent equivalent proportions of time in most behaviors during both baseline sampling and simulated wolf encounters. However, subtle behavioral differences relevant to guarding aptitude emerged. Behavioral divergence between breeds was documented for vigilance, investigation, scanning, and possibly, moving. Interestingly, for the decoy test, breed differences were only detected when the first minute of engagement with a decoy was considered, suggesting that while initial responses may vary among breeds, behavior is more consistent across time in this context. In addition to breed, we found that LGD age and time of day influenced LGD behavior and that sex had no effect on any LGD behavior, all of which corroborate earlier findings on LGD behavior (van Bommel and Johnson, 2012, 2014b; Leijenaar et al, 2015).

Table 6
Model results for all top models (dAICc < 2.0) of the vigilant behavior observed within 60 sec of initial engagement of a livestock guardian dog with the decoy. Results are shown as log odds ratios with standard error shown in parentheses below. Any models that failed to converge are indicated.

	Top vigilant models (first 60 sec)					
	(1)	(2)	(3)	(4)	(5)	(6)
Wolf vs. deer decoy	−2.547	−2.248				−1.796
	(1.579)	(1.486)				(1.236)
Juveniles vs. adults	2.052			2.085		
	(1.373)			(1.508)		
Whitedog vs. kangal					1.380	1.377
					(1.124)	(1.065)
Karakachan vs. kangal					3.245***	2.944***
					(1.549)	(1.440)
Model convergence						
Log likelihood	−44.72	−46.08	−47.44	−46.30	−45.31	−44.12
ΔAICc	0.00	0.15	0.43	0.60	1.19	1.52
Model weight	0.147	0.137	0.119	0.109	0.081	0.069

*p<0.1; **p<0.01
*** $P < 0.05$.

Table 7
Model results for all top models (dAICc < 2.0) of the investigate behavior observed within 60 sec of initial engagement of a livestock guardian dog with the decoy. Results are shown as log odds ratios with standard error shown in parentheses below. Any models that failed to converge are indicated.

	Top investigated models (first 60 sec)		
	(1)	(2)	(3)
Wolf vs. deer decoy		1.012 (0.949)	
Male vs. female			−0.729 (0.828)
Kangal vs. whitedog	2.178* (0.878)	2.091* (0.863)	2.054* (0.864)
Karakachan vs. whitedog	−0.360 (1.346)	−0.209 (1.346)	−0.184 (1.358)
Model convergence			
Log likelihood	−32.39	−31.78	−32.00
ΔAICc	0.00	1.51	1.93
Model weight	0.336	0.158	0.128

**p<0.1; ***p<0.01
* $P < 0.05$.

Regarding baseline LGD behavior, transmontanos were less likely to be scanning than whitedogs (which did not differ significantly from kangals or karakachans) as a proportion of baseline behavior. How this relates to transmontanos' effectiveness as guardians is unclear. It could mean they are less effective at guarding or they use other senses, such as smell and hearing, to detect threats. Our sample size of transmontanos was small relative to the other breeds, creating the possibility that this finding had more to do with the individual transmontanos in our study than the breed at large. There was also a marginally significant trend in baseline data of karakachans moving more than whitedogs. It is unclear whether simply being more active is associated with better guarding behavior, but this behavioral trend may be relevant to sheep producers who move their flocks often or require LGDs to guard large areas.

In the decoy test, neither breed nor decoy type was a significant predictor of any LGD behavior associated with guarding when modeling all behavior observed during testing. In addition, we detected no significant differences in time-to-approach or time-to-leave the decoy as a function of breed, decoy, or other predictor variables. However, when modeling only the behavior observed in the first 60 sec after an LGD engaged with a decoy, we found that kangals were significantly more likely to investigate the decoy than whitedogs (which did not significantly differ from karakachans). There is also evidence that karakachans are more likely to be vigilant than kangals but not whitedogs. Taken summarily, these findings suggest meaningful differences in how LGD breeds respond to potentially threatening stimuli. That kangals were more likely to investigate the decoy may imply a higher willingness for physical engagement. Conversely, karakachans seem to prefer guarding at a distance as indicated by their tendency toward vigilance. Which of these behavioral phenotypes is preferable for deterring predators is likely to be context dependent and will require additional study to disambiguate. Future work should also assess how LGD breed influences sheep survival, which will clarify the practical significance of breed differences in behavior.

That decoy type was not a significant predictor of any of the LGD behavior implies that the LGDs responded to both decoys in the same way. It could mean that the two decoys were perceptually more similar to each other than they were to the animals they were intended to mimic. Anecdotally, LGDs' overall reaction to the decoy types did seem to differ, with more aggressive behavior directed at the wolf decoy (see Fig. 4), but this observation is not supported by statistical analysis. It is difficult to rule out the possibility of crossover interactions because we were unable to test for an interaction of decoy by breed due to our small sample size. However, the main effects for kangals and karakachans discussed earlier may suggest some behavior switching based on decoy type. Importantly, we never observed transmontanos engaging with the deer decoy (see Fig. 4). Although initial response for transmontanos could not be modeled as a function of decoy type, it does imply a strong preference among transmontanos to respond to the wolf decoy, reinforcing our earlier hypothesis that transmontanos may identify threat differently than other breeds. It also suggests that, at least for some LGDs, the decoys were different enough to elicit separate responses. For kangals, karakachans, and whitedogs, decoy similarity could have prompted a general response to novelty rather than eliciting responses based on perceived threat.

Because we imported most of the LGDs in the study as puppies, the majority of behavioral data came from juvenile LGDs (especially for karakachans and transmontanos). Rather than attempting to model only the limited data collected from adult LGDs, we included age as a predictor variable in all our modeling exercises. Conventional wisdom about LGDs suggests that until approximately 2 yr of age, most LGDs are not as effective as their adult counterparts (Dawydiak and Sims, 2004) and some recent research also shows differences in LGD behavior before and after 2 yr (van Bommel and Johnson, 2012). Accordingly, we included a categorical variable of LGD age class in all our models to distinguish between juveniles (< 2) and adults (≥ 2). Age was not a significant predictor of any of the baseline behavior we observed but did predict juvenile LGDs to be more vigilant and have a greater probability of being out of view during the decoy test. We assumed that vigilance would be associated with good guarding skills in LGDs and were somewhat surprised to find it more common among juveniles. However, it may be that more experienced LGDs habituated to the stimulus presented during the decoy test more rapidly while inexperience caused the juveniles to attend to novel stimuli longer (Siwak, 2001). That juvenile LGDs were more likely to be out of view than adults may also be related to experience or, more specifically, confidence. Due to varying habitat characteristics and test protocol, any LGD out of view during a decoy test was > 50 m from the decoy. Actual distance from the decoy was impossible to measure and varied by habitat characteristics, but an LGD could not be both proximate to the decoy and out of view. We believe the out-of-view behavior code may serve as a weak proxy of willingness to approach the decoy. Thus, it may be that juvenile LGDs lack the boldness or willingness of older LGDs to engage with potentially threatening stimuli. Alternatively, out of view may indicate younger LGDs' inexperience and inability to properly assess a threat by moving toward it. If so, our results provide further evidence that LGDs < 2 yr of age lack the abilities of better-performing, older LGDs.

Time of day was also a significant predictor of scanning and general locomotor activity during baseline sampling. These findings are somewhat intuitive and corroborate findings that LGDs are somewhat crepuscular in their activity patterns, or at least not as active during the hottest hours of midday and early afternoon (van Bommel and Johnson, 2014b). This pattern of midday inactivity also corresponds to the time of day in which wolf depredation is least likely (Ciucci and Boitani, 1998).

LGD sex was not a significant predictor of any LGD behavior. Although there exists a sentiment by some who breed and use LGDs that males are more aggressive than females (personal communications), we did not find this to be the case. We had all novel-breed LGDs spayed and neutered at about 1 yr of age to minimize problems of unintentional breeding and wandering. It is possible that intact LGDs may show more divergent behavior patterns between the sexes, but we were unable to test this hypothesis. Nevertheless, our findings corroborate other behavioral analyses of LGDs, which also find no effect of LGD sex on behavior (Leijenaar et al, 2015).

Due to dense vegetation and inconvenient topography, a number of potential observations had to be dropped from our behavioral analyses as certain LGDs remained out of view for the entirety of the decoy test. Although LGDs were always visible to the observer if they were proximate to the decoy, LGD behavior relevant to guarding that took place further from the decoy may have been missed. Although nearly all of the LGDs monitored during the decoy test were equipped with store-on-board GPS collars, those collars were not equipped with accelerometers. Had that been the case, it may have been possible to surmise LGD behavior, even while out of view, by analyzing locomotor activity recorded by the collars. Future field investigations of LGDs may consider employing such technology to partially account for difficulties in viewing behavior in wilderness settings.

Considering the range of behavior we observed, both in baseline sampling and a predator simulation, we found LGD behavior to be mostly the same across breeds. To the extent that the decoys properly modeled threatening and nonthreatening species that LGDs would regularly encounter (i.e., a wolflike canid and a deerlike ungulate), the data presented here suggest that there are no differences in response among kangals, karakachans, or whitedogs to threatening and nonthreatening environmental stimuli. Due to a small sample size and the number of context-specific variables involved in field studies of behavior, it may be more conservative to say that if behavioral differences in how these breeds respond to potentially threatening stimuli do differ, it is in subtle ways that are easily masked by noise in the data. In fact, disregarding decoy type, we did detect subtle breed differences in initial response to the decoy and a significant breed difference in baseline behavior. Additional study will be necessary to determine to what extent these behavioral subtleties are relevant to loss prevention and whether actual loss prevention is a function of LGD breed. It is possible that the small behavioral differences we observed between breeds on approaching the decoy would lead to increasingly divergent behavior if the stimulus was a living animal and not a decoy. For now, our results may help livestock producers make more educated and tailored decisions in choosing the appropriate breed of LGD for their needs and circumstance.

Implications

Wildlife managers, LGD breeders, researchers, and others are frequently asked which LGD breed would work best in a given situation or with a certain predator. While an investigation of sheep mortalities to see which LGD breeds are associated with the greatest loss prevention could help answer this question, understanding behavioral differences among breeds provides information that may be less context dependent (Mehrkam and Wynne, 2014). For this study, we monitored LGD behavior, both passively and in response to a decoy, to determine if LGD breeds show behavioral differences. Our results indicate that few behavioral differences exist among the breeds tested, although kangals tended to be more investigative when engaging a decoy, karakachans more vigilant, and transmontanos more able to decipher a threatening from unthreatening stimuli. While future study will be necessary to see if loss prevention varies by breed, the homogeneity of behavioral data for multiple LGD breeds suggests that regardless of breed, LGDs operate in much the same way. As such, breed may be a less important predictor of a “good dog” than often suggested.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.rama.2018.03.004.

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