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SPECIAL ISSUE: DOGS AND CONSERVATION: CURRENT AND EMERGING CONSIDERATIONS

Interactions between livestock guarding dogs and wolves in the southern French Alps

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Abstract. Thirty years after the return of grey wolves (*Canis lupus*) to the French Alps, the number of livestock losses is on the rise despite livestock guarding dogs (LGDs) being widely used. Their relevance is, therefore, questioned by some sheep owner associations. To date, no study has investigated how LGDs interact with wolves in pastures. We present the results of a 6-year study totalling 3,300 hours of direct night-time observations to record the nature, frequency and outcomes of LGD-wolf interactions in the southern French Alps. We recorded 476 wolf events in the presence of LGDs, including 175 interactions, 66% of which were agonistic. Most (65%) of the interactions occurred at a distance > 100 m from the flock and on average involved more LGDs than wolves. In the presence of LGDs, wolves approached the flocks 134 times resulting in no attack (65%), attacks with no sheep victim (24.6%), or attacks with ≥ 1 sheep victim (10.4%). Our results suggest that LGD-wolf interactions are complex and do not simply occur in the immediate vicinity of the flock. We recommend using groups > 6 LGDs and reinforcing the presence of LGDs in a wider radius around the flock to limit the presence of isolated groups of sheep and to improve protection against wolf attacks.

Key words: agonistic behaviour, *Canis lupus*, extensive small-livestock farming, livestock depredation, livestock protection dogs, thermal imaging

Introduction

Numerous species of large carnivores are threatened worldwide (Ripple et al. 2014), but some populations are also recovering, progressively returning to the areas from which they were once extirpated (Breitenmoser 1998, Karamanlidis et al. 2015). In the early 1990s in Western Europe, improvement in habitat quality, including prey availability, and/or changes in legislation, policy and public attitudes resulted in large carnivores starting to recolonize some historically occupied habitats (Chapron et al. 2014). One of these large carnivores, the grey wolf (*Canis lupus*; wolf), has been expanding its range and increasing in numbers across Western Europe, initially from the Apennines to the French, Swiss and Austrian Alps (Fabbri et al. 2014). Eastern European wolves have also settled in Germany and are recolonizing western Poland and moving westward to Denmark, Belgium and the Netherlands, now forming the Central European lowlands population (Szewczyk et al. 2019). The absence of large wilderness areas in Europe, along with the high adaptability of wolves

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and their ability to disperse over long distances (Ražen et al. 2016) led them to re-establish their populations in highly human-modified landscapes, such as agropastoral systems, and to persist in those rural areas (Llaneza et al. 2012, Milanesi et al. 2017). Sharing space with large carnivores on a continent dominated by humans such as Europe results in conflict with human activities, of which livestock depredation is the most widespread and economically significant (Bautista et al. 2019). Wolves feed mostly on large and medium-sized wild prey (Janeiro-Otero et al. 2020) but can also attack and feed on livestock (Newsome et al. 2016).

Depredation of livestock often results in negative attitudes amongst farmers (Kaltenborn et al. 1999, Dressel et al. 2015) and in the rise of social conflict over wolf management between the stakeholders with strongly diverging points of view and interests (Bisi et al. 2010, Jacobsen & Linnell 2016). Together, this can impair the chances of successful conservation of large carnivores, including wolves (Treves & Bruskotter 2014).

Wolves naturally returned to France from central Italy after their extirpation in the 1930s as a consequence of deforestation, reduction in wild ungulate populations, and human persecution (Lequette & Houard 1995). Between 2017 and 2019, ca. 12,167 heads of livestock were compensated on average each year across the country as a result of possible depredation by wolves (DDT(M)-DREAL Auvergne-Rhône-Alpes 2020a). Sixty-two percent of these compensations were paid in the Provence-Alpes-Côte d'Azur (PACA) region (DDT(M)-DREAL Auvergne-Rhône-Alpes 2020a), which covers 49% of the wolf distribution area. Wolves have had full legal protection in France since 1993, but the Ministry of the Environment can issue permits to remove individuals at any time. Thus, in 2019, 94 wolves were legally culled in France out of a maximum of 100 authorized (DDT(M)-DREAL Auvergne-Rhône-Alpes 2019). The authorization has been renewed for 2020 for 90 more wolves out of a population of ca. 580 (OFB 2020). In PACA, approximately 1,500 sheep farmers are present with a total of ca. 786,000 sheep (Chambres d'agriculture Provence-Alpes-Côte-d'Azur 2018). During the summer transhumance, ca. 550,000 sheep move from the lowlands of southern France towards the southern Alps and ca. 140,000 towards the northern Alps where they spend four to five months on mountain pastures (Maison Régionale de l'Elevage – Sud PACA 2019). On the Canjuers Plateau (Fig. 1), pasture grazing lasts eight to nine months, from spring to autumn. During this time, sheep are at the highest risk of depredation by wolves but some flocks remain outside all year round and can suffer attacks throughout the year. Following the extirpation of wolves from the southern Alps by 1900, livestock protection measures (i.e. permanent herding, use of livestock guarding dogs and night penning) were dropped in the region. This increased the vulnerability of flocks to wolf attacks during the recolonization phases (Gervasi et al. 2020), which was possibly worsened by weakened anti-predatory behaviour of livestock (Flörcke & Grandin 2013). The return of the wolf to the French Alps has thus forced livestock farmers and shepherds to resume the protection of their flocks from large carnivore attacks.

Livestock guarding dogs (LGDs) have been used across the world to protect livestock from various species of predators, from felids (e.g. cheetah *Acinonyx jubatus*) and canids (e.g. coyote *Canis latrans*) to ursids (e.g. brown bear *Ursus arctos*) and even primates (e.g. baboons *Papio* spp.; Gehring et al. 2010). In Europe, they have been used for over 2,000 years to prevent livestock depredation from wolves (Coppinger & Coppinger 1993). LGDs are some of the last domestic dogs to remain in contact with their ancestral counterparts (wolves) and both are constantly interacting on pastureland, either indirectly (olfactory, visual and auditory contacts) or directly (physical encounters). To date, most studies focusing on the interactions between LGDs and wild predators have relied on indirect information such as farmers' memory, reports and anecdotes (Green et al. 1984, Marker et al. 2005a, b, Potgieter et al. 2013, 2016, Leijenaar et al. 2015, Whitehouse-Tedd et al. 2020) or, recently, on the analysis of LGDs diet (Drouilly et al. 2020, this special issue).

Although anecdotal evidence has value because it reports on behaviour that is rarely directly observed on pastures, it is too rare and scattered to allow for an understanding of the way LGDs interact with wild predators, including wolves. In the southern French Alps, wolf depredation on sheep grazing extensively on pastures is a serious challenge for livestock owners and shepherds, and losses have been increasing despite the widespread use of LGDs. Our aim was therefore to determine the nature, frequency and outcomes of LGD-wolf interactions to advance our understanding of

LGD and wolf behaviour in the alpine pastoral context. Our novel night-monitoring protocol using thermal imaging technology enabled us to directly observe the events occurring on summer pastures at night and to explore LGDs' behavioural responses to wolf presence (see www.ipra-landry.com/en/ressources-references/videos-canovis/ for some examples of videos). We hypothesized that LGD group size and the distance from the flock at which LGD-wolf interactions occurred would both be important variables to consider for better protection of flocks facing potential wolf attacks. Based on a review of the international literature, we predicted that higher numbers of LGDs would provide better protection to the flock (Green et al. 1994, van Bommel & Johnson 2012, Allen et al. 2017), and our specific objectives were to determine the minimum effective number of LGDs in our system and the underlying mechanism through which better protection could be achieved. We also predicted better protection of the flock if LGDs remained in its immediate vicinity, as highlighted in the theoretical literature (Coppinger et al. 1983, Lorenz & Coppinger 1986). Although our results are preliminary, they offer novel insights into the relationships between LGDs, flocks and wolves. We conclude by making some management recommendations to improve the protection of sheep flocks with LGDs in order to promote a shared landscape with wild carnivores.

Material and Methods

Study area

Our study was mainly conducted at two sites situated in the Provence-Alpes-Côte d'Azur region in south-eastern France (Fig. 1). In the Var Department, the Canjuers Plateau (site 1) covers 35,000 ha of extensive pastureland, ca. 50 km to the north of the city of Draguignan (Fig. 1, Table 1). The topography is a mixture of plateaux, small valleys and hills with an elevation ranging from 586-1,577 m a.s.l., surrounded by mountain ranges (Fig. 1). The warm and dry Mediterranean climate supports vegetation in the form of Mediterranean shrubland (garrigue, 18%) with some downy oak (*Quercus pubescens*), Scots (*Pinus sylvestris*) and Aleppo (*Pinus halepensis*) pine forests covering the surrounding mountains (65%, Observatoire de la forêt méditerranéenne 2003). Air temperatures can be extreme (–20 °C in January and 30 °C in July) with the annual precipitation ranging in 900-1,300 mm (Charrier et al. 2019). In the Var Department, wolf depredation on sheep has been increasing over the past nine years with 1,117 sheep losses found and compensated by the French Government in 2019 (DDT(M)-DREAL Auvergne-Rhône-Alpes 2020b). In recent years, 6.6% of the grazing flock of the Canjuers Plateau has been lost to wolf depredation, representing ca. 60% of the losses in the Var Department and making it one of the highest in Europe (Blanchon et al. 2018). For this reason, the Canjuers Plateau has been termed "the wolf factory of the Var" by small-livestock farmers (Blanchon et al. 2018). Canjuers hosts the largest military camp in Europe, sharing the landscape with six *regroupements pastoraux*; a collective farming system that involves communal grazing of multiple herds, for a total of 61 grazing units (Blanchon et al. 2018). A total of 200 cattle and ca. 14,000 ewes and goats belonging to ca. 30 small-livestock farmers grazed extensively on 17,000 ha of the military camp (ca. 49% of the Canjuers Plateau), protected by 137 LGDs in 2017 (Blanchon et al. 2018). Some farmers combine their livestock, resulting in flocks of 1,500-2,000 animals. During our study, two to three wolf packs were thought to be using the area, representing a total of ca. 10 to 15 adult individuals.

The Mercantour Mountain Range (site 2) is situated ca. 70 km to the north of the city of Nice (Fig. 1, Table 1). It includes the Mercantour National Park that covers 214,670 ha, 46% of which is used for extensive grazing in the form of 177 alpine pastoral units (i.e. alpine pastures where a particular sheep flock is grazed during the summer season; Parcs Nationaux de France 2012). The topography is complex, with steep-sided narrow valleys and canyons. Altitudes range from 500 to 3,000 m a.s.l. The vegetation consists mostly of European larches (*Larix decidua*), holm oaks (*Quercus ilex*), Mediterranean olive trees (*Olea europaea*), rhododendrons (*Rhododendron ferrugineum*) and alpine meadows sometimes interspersed with fir and spruce forests (Fig. 1). The climate is affected by the Mediterranean Sea so rainfall is abundant (generally above 1,000 mm/year) and can be torrential with storms (www.maritimemercantour.eu). During summer, between 120,000 and 140,000 sheep graze extensively on pastures in the park, and between 60,000 and 70,000 sheep graze in the park all year round (B. Lequette, pers. comm. to Kaczensky 1996).

Additionally, in 2018 we monitored another site in the Drôme Department of the Auvergne-Rhône-Alpes region (site 3; Fig. 1, Table S1). This site is

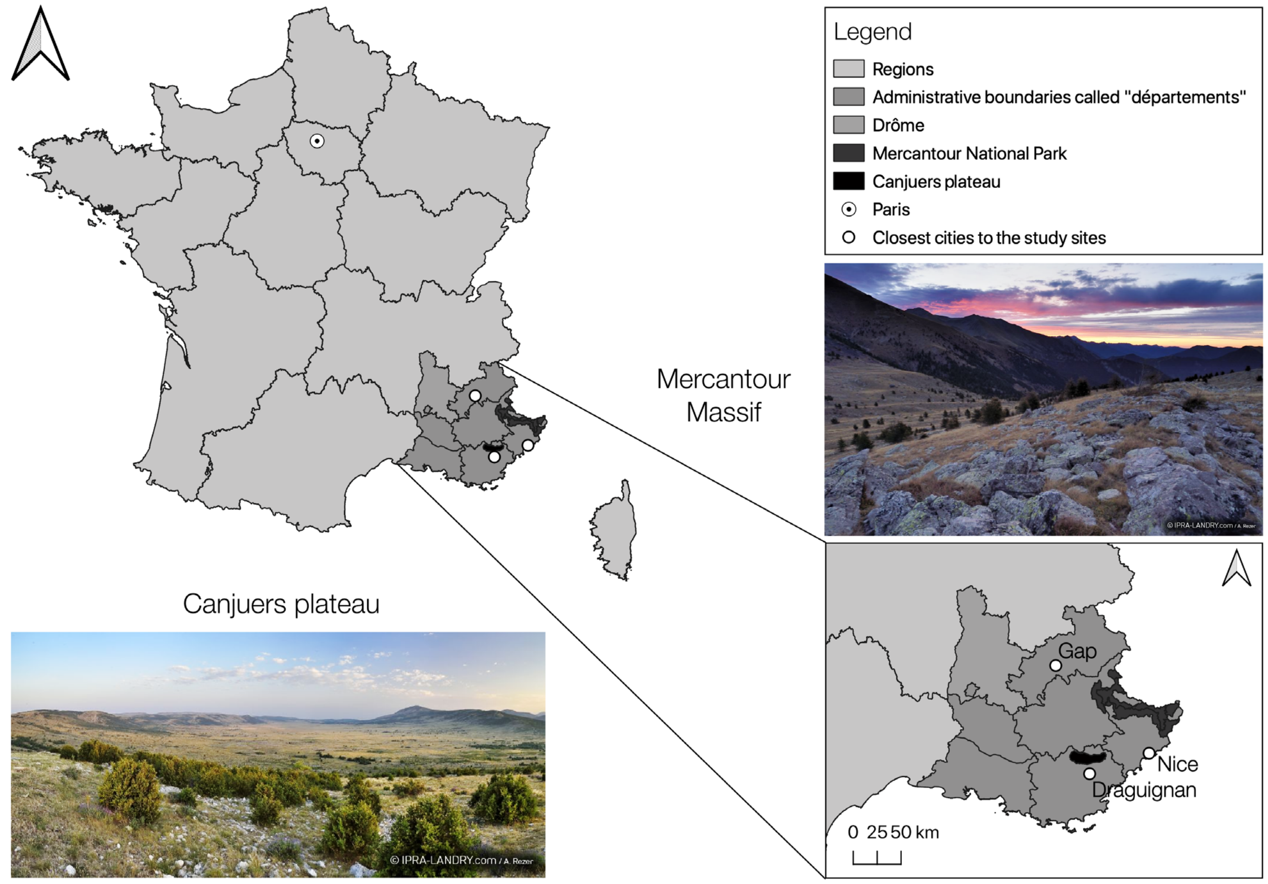

Fig. 1. Map of France with the Provence-Alpes-Côte d'Azur (PACA) region and the Drôme Department highlighted in the darkest shades of grey. The polygons of the Mercantour National Park and the Canjuers Plateau are in dark grey and black, respectively. The closest cities to the study sites are represented with white dots. The pictures illustrate the typical landscapes of the pastoral units in the Canjuers Plateau and the Mercantour Massif.

at the junction between the northern and southern French Alps, within the southern borders of the Vercors Regional Nature Park. The vegetation consists of meadows and Ericaceae moors with some patches of pine and larch forest. Altitudes range from 1,300-1,900 m a.s.l. In 2018, this site was in the core of the home range of a breeding pack of wolves (Borelli & Landry 2018).

These three sites were chosen for two main reasons: 1) they were the first to be re-colonized by wolves in the 1990s, and 2) together, they currently represent ca. 33% of the national livestock losses from wolf depredation, despite the high level of livestock protection and farmers' efforts to adapt their practice to the presence of this predator. The three sites are also representative of the typical pastoral landscapes most impacted by wolf depredation in France and more generally in the southern Alps. We monitored a total of 12 grazing units (four in the Canjuers Plateau, seven in and around the Mercantour National Park and one in the Haut Buëch in the Drôme Department), each extensively grazed by one or more sheep flocks. Five units (three in the Canjuers Plateau and two in and around the Mercantour National Park) were intensively monitored for five (2014-2018) and six (2013-2018) years, respectively (Table 1). The six other units were monitored less intensively between 2013 and 2015 and the Haut Buëch site (Drôme) was monitored in 2018 only (Table S1). Each field session lasted between two and ten consecutive days, depending on environmental conditions, farmers' planning, logistics and wolf presence.

Night-time monitoring of LGD-wolf interactions

Thermal imaging technology is the process of converting infrared (IR) radiation (heat) emitted from an object into visible images that depict the spatial distribution of temperature differences in a scene viewed by a thermal camera (Speakman & Ward 1998). Developed by the military, it needs no light to be effective and allows the detection of animals at distances > 500 m (Focardi et al. 2001). It is being increasingly used in wildlife monitoring

Table 1. Characteristics of the five intensively-monitored mountainous extensive grazing units in and around the Mercantour National Park (M1-M2) and in the Canjuers Plateau (C1-C3), France.

Pastoral unit	M1	M2	C1	C2	C3
Flock size	1,500-1,700	2,500	1,800-2,000	1,600-1,800	1,200-1,400
Human surveillance	Full-time farmer or shepherd	Full-time farmer or shepherd	Occasional visits by the farmer and daily visit by the shepherd	Occasional visits by the farmer or shepherd	Full-time shepherd
LGD breed	Pyrenean mountain dogs	Cross-breed: Pyrenean × Abruzzese, Pyrenean mountain dogs	Cross-breed: Pyrenean × Anatolian, Pyrenean × Estrela; Estrela mountain dogs, Pyrenean mountain dogs, Anatolian shepherd dogs	Pyrenean mountain dogs	Pyrenean mountain dogs, Anatolian shepherd dogs
Flock husbandry	Guarded	Guarded	Free-range, initially guarded	Intermittently guarded	Guarded
Elevation (m a.s.l.)	2,000-2,600	1,900-2,300	800-1,200	800-1,200	800-1,200
Habitat	Meadows	Meadows and larch forest	Woodland and shrubland growing on acid soil	Woodland and shrubland growing on acid soil	Woodland and shrubland growing on acid soil
Equipment	3 mountain huts, 2 enclosures for sorting sheep and care	3 mountain huts, 1 enclosure for sorting sheep and care, water troughs	1 enclosure for sorting sheep and care, water troughs	1 mountain hut, 1 enclosure for sorting sheep and care, water troughs	1 mountain hut, water troughs
Sheep protection methods	3-5 LGDs, completely closed night pen, or half enclosed night pen, or flock gathered but not enclosed at night	10-14 LGDs, completely closed night pen, or half enclosed night pen, or flock gathered but not enclosed at night	10-25 LGDs, flock gathered but with different independent bedding sites chosen by the sheep	8-11 LGDs, flock gathered with a common bedding site chosen by the sheep	6-9 LGDs, completely closed night pen
Monitoring period	June-October	July-October	June-October	June-October	July-September

studies as it can substantially reduce or suppress disturbance and fleeing of wildlife, improving monitoring and data collection on cryptic, nocturnal homeotherm species in their natural habitats (Allison & Destefano 2006, Havens & Sharp 2016). To our knowledge, this is the first time that this technology has been used to elucidate interactions between wolves and LGDs in human-dominated landscapes. Two pairs of high-end MATIS long-range cooled (–200 °C) infrared binoculars (© SAFRAN Electronics & Defense, previously SAGEM Défense Sécurité), each coupled to an external mini digital video recorder, were used to film night-time LGD-wolf interactions on summer pastures. We classified the types of response displayed by LGDs during LGD-wolf interactions into four categories: agonistic, searching for wolves on the pasture, non-belligerent, and vocalization (Table 2). Each category contained specific types of behaviour that LGDs might display on their own

Table 2. Description of the four response categories and twelve different associated types of behaviour displayed by livestock guarding dogs (LGD) during interactions with wolves on pastoral units in the southern Alps, France (2013-2018).

LGD response category	LGD behaviour	Behaviour description
Agonistic	Interposition	The LGD and the wolf face off
	Chasing off	The LGD runs towards the wolf and stops once the wolf runs away
	Pursuit	The LGD runs after a wolf that is running away
	Fight	The LGD physically fights against the wolf
Searching for the wolves	Wandering	The LGD is walking or trotting around the pastoral unit
	Moving towards the source of disturbance	The LGD moves towards the place where disturbance is occurring/has just occurred
	Tracking	The LGD follows a wolf trail sniffing the air or the ground
Non-belligerent	Tolerance	The LGD does not react directly to wolf presence nearby (they keep a visual contact)
	Social investigation	The LGD allows the wolf to sniff different parts of its body
	Invitation to play	The LGD and/or the wolf invite each other to play (play bow or chase invitation)
	Escort at a distance	The LGD walks parallel to the wolf (80 to 150 meters apart)
Vocalisation	Barking	The LGD barks with no other noticeable behaviour

(e.g. barking) or as part of a behavioural sequence (association of at least two types of behaviour displayed by LGDs when wolves are present on the pasture, e.g. barking and chasing). A behavioural sequence started when the LGD(s) responded to wolf presence in the pastoral unit, and ended either when the LGD-wolf interaction left our field of observation, or when the LGD(s) returned to the flock after the wolf/wolves left the area under the LGDs' protection.

From dusk to dawn, two to three observers stationed between 300 and 700 m from the flock took shifts to scan the sheep and their surroundings (up to 5 km) with a pair of infrared binoculars. Depending on the landscape complexity, each scan lasted between two and ten minutes with a one- to three-minute break between each scan. Each time a wolf was observed in the pastoral system (i.e. wolf event), we watched and videoed the scene and noted 1) whether LGDs were visible and with the flock, 2) what the wolves were doing, including whether they showed any interest in the pastoral system (i.e. flock, LGDs or infrastructure), 3) how the LGDs and wolves reacted to each other's presence (i.e. response type and behaviour, Table 2), 4) how many LGDs and wolves were involved in each interaction, 5) the distance of each LGD-wolf interaction from the flock, and 6) the outcome of each LGD-wolf interaction. After fieldwork, observers extracted relevant information from field notes and videos. An approximate distance of each LGD-wolf interaction from the flock was estimated remotely using Google Earth (Gorelick et al. 2017) or calculated after collecting the GPS coordinates of each interaction in the field with a handheld GPS. In the morning, when possible, fieldworkers gave feedback to the farmer or the shepherd about the night's events.

Data analysis

We calculated the relative frequency of occurrence of each type of behaviour displayed by LGDs in the presence of wolves (Table 2) as the number of times a specific type of behaviour occurred divided by the total number of times all types of behaviour occurred, expressed as a percentage. We also recorded the frequency with which each type of behaviour occurred as part of a behavioural sequence. We used chi-square contingency tests to determine whether the different types of behaviour of LGDs in the presence of wolves were independent. In particular, we were interested in the relationship between specific types of behaviour (as presented in Table 2) and LGD group size (i.e. ≤ 6 or > 6 dogs), distance of the LGD-wolf interactions from the flock (i.e. from 0 to > 1,000 m), and presence (yes/no) on the pasture of

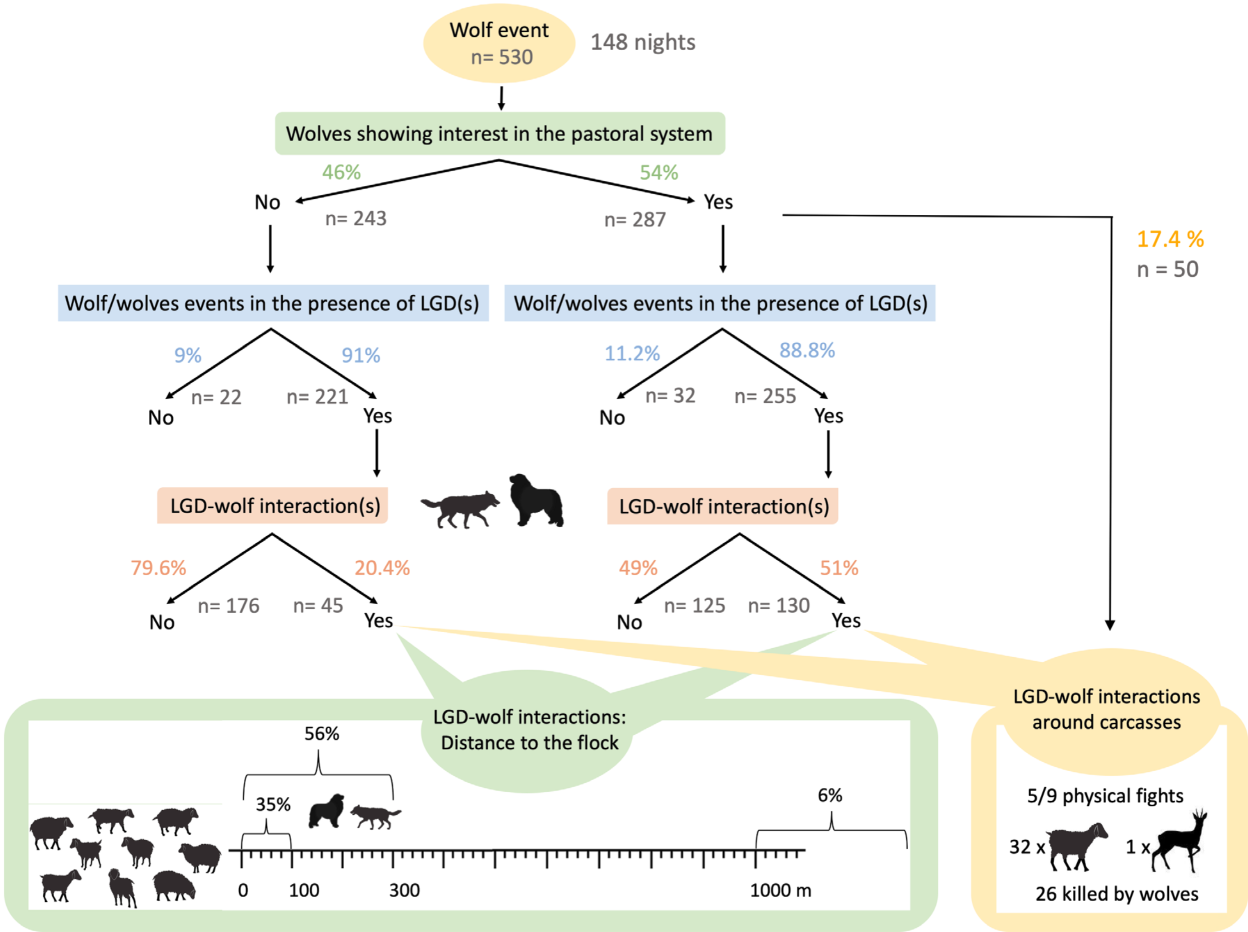

Fig. 2. Hierarchical diagram summarising how wolf events lead to interactions between livestock guarding dogs and wolves, the distance of these interactions from the flock and the special case of carcasses present on pastures in the southern French Alps.

a domestic or wild animal carcass, either killed by the wolves or having died from another cause. We used non-parametric one-tailed Mann-Whitney U tests to test whether (1) fights would involve more LGDs and more wolves than any other type of LGD-wolf interactions, and (2) large (> 6) groups of LGDs would have more dogs involved in LGD-wolf interactions than small (≤ 6) groups. We also used a Spearman correlation to test whether there was an association between the number of LGDs and the number of wolves involved in LGD-wolf interactions (i.e. as the number of wolves increased in an LGD-wolf interaction, so did the number of LGDs). Finally, we used Chi-square contingency tests to compare the frequency of attack and predation when sheep were in small isolated groups (i.e. situated at a distance > 300 m from the flock and for more than four hours at a time) *vs.* with the flock. We used Mann-Whitney U tests to determine whether the mean number of wolves, LGDs and LGD-wolf interactions were different during an attack with victim(s) *vs.* without victims (i.e. sheep being depredated). Means are presented ± SD as a measure of variation. For all tests, we assessed our results at the level $\alpha = 0.05$.

Results

Between 2013 and 2018, we spent 291 nights in the field (130 in the Mercantour, 133 in Canjuers and 28 in Drôme), representing ca. 3,300 hours of nocturnal observations between our 12 grazing units. A total of 530 wolf events (124 in the Mercantour, 378 in Canjuers and 28 in Drôme) were recorded over 148 nights. Ninety percent of these events (n = 476) occurred in the presence of at least one LGD in the flock or in its immediate surroundings (Fig. 2). Wolves showed interest towards the pastoral system in 54% of the wolf events, representing 74% of the total LGD-wolf interactions we were able to record (Fig. 2). The rest of the time (46%), wolves were present in the pastoral unit without showing interest in the pastoral system. These types of wolf events could still trigger a response from the LGD(s) and accounted for 26% of the total LGD-wolf interactions (Fig. 2).

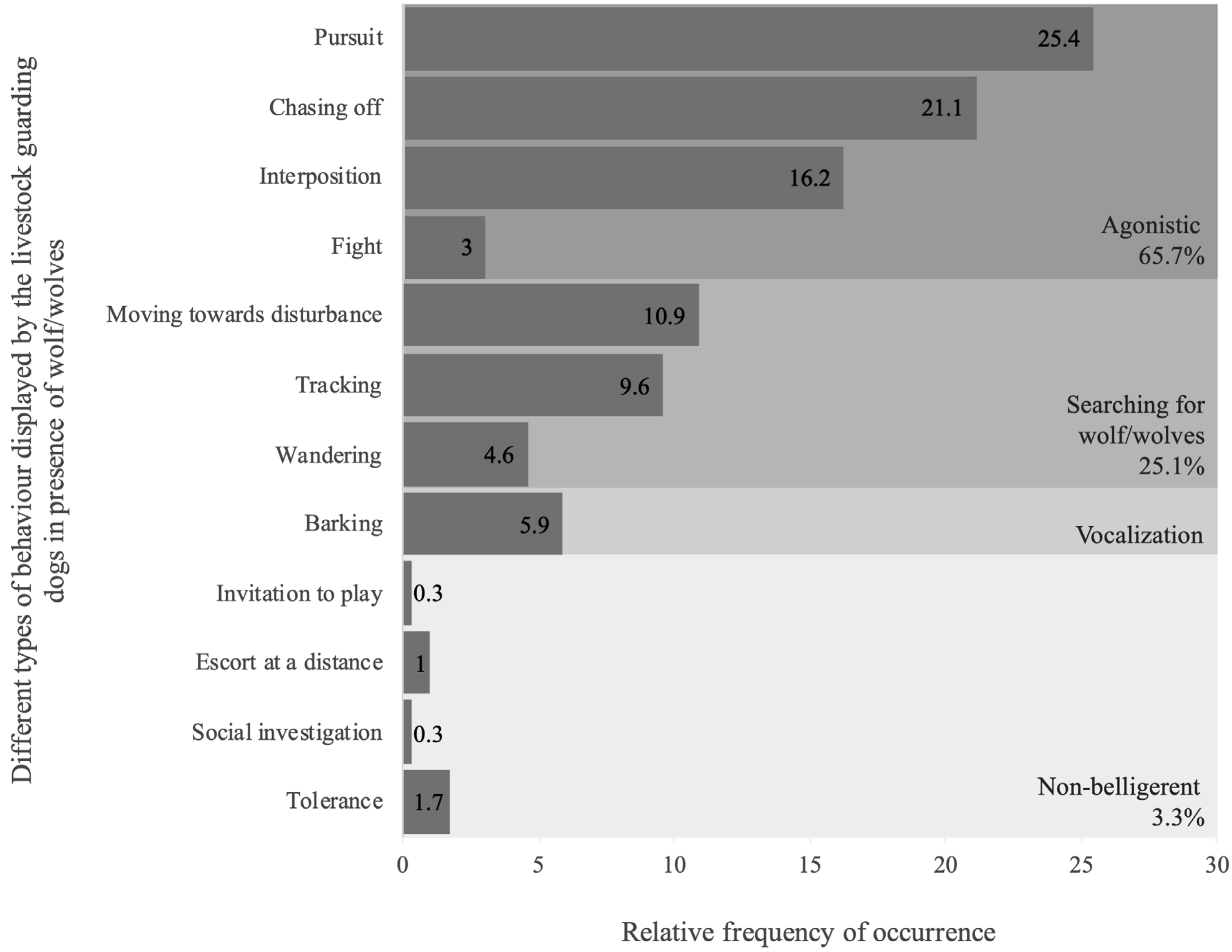

Fig. 3. Histogram of the relative frequency of occurrence (in %) of twelve different types of behaviour displayed by livestock guarding dogs in the presence of wolves on summer pastures in the southern French Alps. The twelve types of behaviour are divided into four broad response categories highlighted with their frequency (in %) on the right-side of the graph.

Nature and frequency of LGD-wolf interactions

About a third (n = 175) of the wolf events triggered a response from at least one LGD, resulting in LGD-wolf interactions (Fig. 2). Agonistic behaviour was significantly more frequent (65.7%, $\chi^2 = 59.65$, $P < 0.001$) than the three other types of behaviour pooled together (34.3%; Fig. 2). It was present in 72% of all behavioural sequences. LGD-wolf interactions resulted in LGDs chasing wolves off (21.1%) and pursuits were present in 44.2% of the behavioural sequences. Physical fights between LGD(s) and wolf/wolves occurred in nine different cases (Table S2). No LGD was wounded but we were unable to check whether wolves were injured. LGDs' searching behaviour represented 25.1% of individual behaviour (Fig. 3) but occurred in 43.7% of the behavioural sequences. Non-belligerent responses were uncommon (3.3%; Fig. 3) and occurred in 5.7% of the behavioural sequences. The wind and the distance between the observers and the interactions did not always allow the recording of vocalizations (i.e. barking and other sounds such as growling) but barking accompanied another behaviour in a behavioural sequence in at least 59% of the LGD-wolf interactions.

Number of LGDs and wolves involved in interactions

We were able to count the number of LGDs and wolves involved in LGD-wolf interactions in 92% and 95% of the cases, respectively. In the majority of LGD-wolf interactions (74%), LGDs faced a single (56%) or two wolves (18%) and in only three cases (< 2%) did LGDs have to face a maximum of seven wolves (in Canjuers). On average, 3.4 ± 2.8 LGDs (range: 1-20) and 2.0 ± 1.5 wolves (range: 1-7) were involved during LGD-wolf interactions. Physical fights between LGDs and wolves involved significantly more LGDs (U = 1135.5, $P = 0.002$) and more wolves (U = 1385.5, $P < 0.001$) than any other interactions, with an average of 7.1 ± 3.6 LGDs (range: 1-13) and 5.3 ± 1.8 wolves (range: 2-7; Table

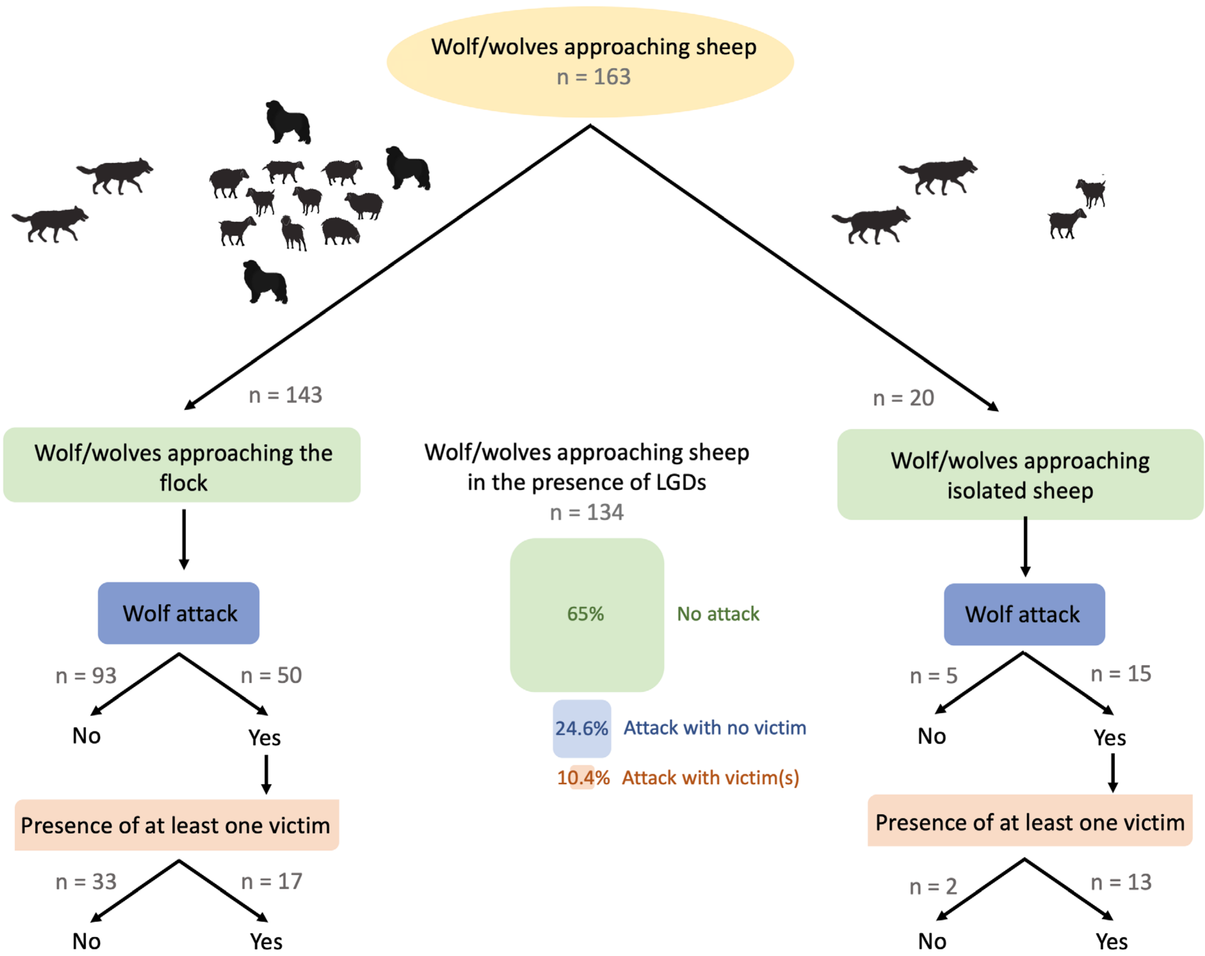

Fig. 4. Hierarchical diagram summarising the different outcomes occurring when wolves approach sheep (flock or isolated small groups) on summer pastures in the southern French Alps.

S2). LGDs in packs ≤ 6 individuals (n = 30) were less likely to run after wolves (χ^2 = 51.98, P < 0.001) than LGDs in packs > 6 individuals (n = 132). During an LGD-wolf interaction, packs with more than six LGDs were significantly more likely (χ^2 = 17.46, P < 0.001) to have dogs remaining with the flock than packs with ≤ 6 LGDs (87% *vs.* 54%). The number of LGDs involved in LGD-wolf interactions was significantly smaller (U = 1306.5, P < 0.001) in packs ≤ 6 dogs than in packs > 6 individuals (median: 2 *vs.* 3; mean: 2.1 ± 1.2 *vs.* 3.8 ± 3.0 LGDs). There was a weak but significant positive association between the number of wolves and the number of LGDs involved in LGD-wolf interactions (ϱ_{160} = 0.21, P = 0.008).

Distance of LGD-wolf interactions from the flock

LGD-wolf interactions occurred at different distances from the flock, ranging from < 100 m to > 1000 m, but most of LGD-wolf interactions (56%) began at a distance < 300 m from the flock, including 35% at a distance < 100 m (Fig. 2). Only 6% of the LGD-wolf interactions occurred at a distance > 1000 m (Fig. 2). The proportion of pursuits was not statistically higher (χ^2 = 3.04, P = 0.080) when LGD-wolf interactions started nearer to the flock (i.e. between 0 and 300 m) than when they started at a distance > 300 m.

The particular case of carcasses

LGD-wolf interactions around carcasses amounted to ca. 17% of the wolf events and represented 50 interactions around 33 different carcasses (32 of domestic animals and one of a roe deer (*Capreolus capreolus*), 26 of which were killed by wolves; Fig. 2). Up to six wolves (mean: 1.9 ± 1.5) and 12 LGDs (mean: 3.5 ± 2.8) met around a single carcass. It is around carcasses that the most intense LGD-wolf interactions were observed, accounting for five of the nine physical fights (Fig. 2, Table S2). The proportion of LGD responses with at least one type of agonistic behaviour in the sequence was significantly higher (χ^2 = 4.41, P = 0.036) when a carcass was at stake than in any other situation (86.0% *vs.* 71.3%). In five cases, though, LGDs tolerated wolves scavenging on a carcass at a short distance from the flock.

Outcomes of LGD-wolf interactions

In the presence of LGDs, wolves approached the flocks 134 times resulting in no attack 65% of the time (i.e. the wolves retreated), in attacks with no victims (24.6%) or in attacks with at least one victim (10.4%; 1.3 kill per attack on average, range: 1-4; Fig. 4). There was no significant difference in the mean number of LGDs (U = 468.5, P = 0.459) or wolves (U = 290.5, P = 0.303) involved during an attack with or without victims. However, there were significantly more attacks (75% *vs.* 35%; χ^2 = 11.635, P < 0.001) and more attacks with victims (86.7% and 34.0%; χ^2 = 12.696, P < 0.001) when sheep were in small isolated groups than when they remained with the main flock. There were also significantly more LGD-wolf interactions during wolf attacks without victims than during attacks with victims (χ^2 = 23.48, P < 0.001). There was a significantly lower number of wolf events without LGD(s) during attacks without victims than during attacks with victim(s) (χ^2 = 10.50, P = 0.001).

Discussion

The aim of this study was to determine the nature, frequency and outcomes of the interactions between livestock guarding dogs and wolves on summer pastures. The intrinsic characteristics of wolves make them difficult to study (Mech 1981), particularly in human-dominated landscapes such as those of Western Europe. To our knowledge, our study is the first to make use of thermal imaging technology to observe wolves directly and to study their nocturnal interactions with dogs protecting their flocks on pastures. The fact that we recorded so many wolf events strongly suggests that wolves are ubiquitous in the pastoral system and that livestock guarding dogs, sheep flocks and wolves share a common living space where their activities overlap.

Wolf attacks with sheep victims *vs.* no victims

Three variables appeared to decrease the risk of wolf predation on sheep: the gregariousness of the sheep (flock *vs.* small isolated group) on the pasture, the presence of livestock guarding dogs, and the ability of the dogs to interact with wolves. We found that sheep that were part of small isolated groups were at higher risk of attack and higher risk of predation than sheep who remained with the flock. These results can certainly be explained by the presence of livestock guarding dogs with the flock, which is not always the case when sheep are isolated. In addition, flocks present increased vigilance and thus probability of predator detection compared to small groups (the many-eyes hypothesis; Lima 1995), as well as dilution of risk due to the presence of more individuals (Pulliam 1973). In our study sites, when the sheep detected wolves approaching the flock, their movement and the change in the general sound of their bells alerted the dogs who moved quickly towards the source of the disturbance, generally barking. In small isolated groups, wolves are also able to detect and focus more easily on one individual to attack (Vine 1971). Flocking is a common evolutionary response of herbivores to predation risk as gregariousness increases safety (i.e. "safety in numbers"; McNamara & Houston 1992), and is found in many species worldwide, including wild sheep (e.g. Rieucau & Martin 2008). Having enough dogs on the pasture to limit the formation of isolated unguarded groups of sheep is therefore crucial to minimise wolf attacks and predation. We also showed that wolf events without livestock guarding dogs led to more sheep being attacked than wolf events in the presence of dogs. This shows that the presence of dogs still decreased predation risk (i.e. primary repellent), even if it was not always sufficient to avoid an attack or a kill. During a wolf attack, the number of interactions with the dogs also played an important role. Far less predation occurred when there were more interactions between the wolves and the dogs. Constant harassment of the wolves by the dogs might result in wolves needing to expend more energy and take more risk to make a kill. These repeated interactions might in the end discourage some wolves from killing sheep and show how important attentiveness and protectiveness are when raising and training those dogs (Lorenz & Coppinger 1986).

Interactions between livestock guarding dogs and wolves and the number of dogs

Wolf events did not always trigger a response from the dogs (Fig. 2), mostly because wolves were not threatening the flocks, but also because the dogs did not always notice the wolves, or were in another area of the flock when wolves approached. Nonetheless, direct and indirect interactions between livestock guarding dogs and wolves were frequent at our study sites. As expected, most interactions were agonistic but lethal encounters between livestock guarding dogs and wolves were rare. We did not observe any such behaviour directly during our study but two sheep farmers working with us reported the death of an adult livestock guarding dog killed by wolves in the Mercantour Massif and the death of a young and an adult livestock guarding dog during the same fight in Canjuers. A sub-adult wolf was also reported to have been killed by livestock guarding dogs in Canjuers. The rarity of these lethal encounters seems to be in line with the intrinsic characteristics of both livestock guarding dogs and wolves. Coppinger & Schneider (1995) characterised livestock guarding dogs as being "brave animals" protecting their flock while also minimizing lethal encounters. They described their actions as disrupting wolf predatory behaviour. Yet, on some occasions, livestock guarding dogs have also been reported to kill predators. In Turkey for example, Anatolian shepherd dogs were reported to kill wolves (Urbigkit & Urbigkit 2010). In most of these reports, livestock guarding dogs killed predators that were smaller than them. In a study conducted in Namibia, farmers reported that livestock guarding dogs killed black-backed jackals (*Canis mesomelas*), baboons (*Papio* sp.), caracals (*Caracal caracal*), bat-eared fox (*Otocyon megalotis*), African wildcat (*Felis sylvestris*) and cheetah (*Acinonyx jubatus;* Potgieter et al. 2016), all smaller than the typical livestock guarding dogs size. Similarly, wolves were depicted in multiple reports reviewed by Mech (1981) as displaying "aversion to fighting" and "avoiding aggressive encounters with dogs", which might explain why the number of attacks with victims was lower when dogs harassed wolves through numerous interactions. At our study sites, wolves were almost always outnumbered by dogs. According to Boitani (1983), wolves tend to live in pairs or small packs in areas where they are highly persecuted (ca. 15% of the wolf population has been lethally controlled each year in France since 2018), which is a handicap when facing large groups of livestock guarding dogs. In our study sites, fights only occurred between larger packs of wolves and livestock guarding dogs. These facts might explain why we recorded no lethal encounters during our nocturnal observations and it would be interesting to monitor whether lethal encounters start emerging when/if wolf packs become larger. Wolves killing dogs, including livestock guarding dogs, even if rarely intense, is widespread (Bangs et al. 2005, Mertens & Schneider 2005, Lescureux & Linnell 2014), notably when dogs are outnumbered by wolves (Ciucci & Boitani 1998, Iliopoulos et al. 2009, van Liere et al. 2013). Such extreme interactions might damage the perception of wolves and discourage farmers from getting more livestock guarding dogs, which could threaten the coexistence between farming activities and wolf conservation (Skogen & Krange 2003, Lescureux & Linnell 2014).

Coppinger & Schneider (1995) also mentioned that livestock guarding dogs could display complex, ambiguous behaviour, that sometimes seems maladapted (e.g. social investigations, invitations to play). At our study sites, interactions between livestock guarding dogs and wolves were not always agonistic, and tolerance, social investigation, escort at a distance and even invitation to play were recorded. These non-belligerent interactions, although rare, might lead to potential hybridization (Vilà & Wayne 1999, Hindrikson et al. 2012), which is a major source of concern for wolf conservation in Europe (Hindrikson et al. 2017), and/or disease and parasite transfer (de Almeida Curi et al. 2010, Müller et al. 2011) between livestock guarding dogs and wolves due to their genetic proximity. The number of livestock guarding dogs facing wolves might therefore play an important role in avoiding the three extreme cases cited above (i.e. interactions resulting in death or hybridization and/or disease transfer), with the assumption that the more dogs, the less risk of extreme behaviour there would be. Our study highlighted the importance of the number of livestock guarding dogs present in or around the flock. In accordance with our first hypothesis and prediction, larger groups of livestock guarding dogs offered better protection to the flock but not directly by decreasing the number of attacks with victims. Rather, larger groups allow for the creation of a buffer zone between the wolves and the flock, preventing attacks from occurring. Some dogs formed the outer boundaries of the buffer zone by engaging in pursuits with wolves far from the flocks while others formed the inner boundaries of the buffer zone by staying with the sheep. High numbers of dogs are also useful in increasing the number of interactions with wolves, which is one of the mechanisms through which the frequency of attacks with victims seemed to decrease at our study sites. High numbers of dogs are used in the Canjuers Plateau in particular, because flocks roam freely all day long without any permanent herding and are generally not penned at night. This particular way of keeping sheep must therefore be compensated by a high number of dogs. Another advantage of having a large group of dogs is that the group can be structured as an age pyramid, with young learning dogs (to replace the old ones), mature working dogs, and old working dogs. Thus, a minimum number of seven livestock guarding dogs (two-three-two) makes the most sense in terms of age structure while maximising protection.

Although most interactions between livestock guarding dogs and wolves were agonistic, wolves kept returning to the pastoral units. Livestock guarding dogs may therefore be seen as primary repellents (Shivik et al. 2003), disrupting wolves' behaviour (Coppinger et al. 1988), but unable to permanently modify it through associative learning, suggesting that no long-term avoidance was occurring at our study sites. Livestock guarding dogs were thus able to minimize but not completely suppress negative impacts on livestock.

Towards a new definition of livestock guarding dogs – flock bonding on free-range pastures

Some publications discuss the average distance between livestock guarding dogs and sheep on rangeland (Young et al. 2019, Mosley et al. 2020). Livestock guarding dogs have occasionally been found to roam far from their sheep (van Bommel & Johnson 2014b, Mosley et al. 2020). In a study using audio playbacks and scent placements to simulate incursions by dingoes (*Canis dingo*) at different locations within livestock guarding dog ranges, the authors found that the dogs moved up to 570 m away from the sheep they were guarding to challenge a perceived intruder inside their range (van Bommel & Johnson 2014a). No study so far has been able to observe and record the presence of potential predators and the distance from the flock at which dogs interacted with them.

Our results demonstrate that interactions between livestock guarding dogs and wolves regularly occur at some distance from the flock (> 300 m). Even if there were no wolf attacks 65% of the time when wolves approached the flocks, almost three out of 10 attacks were in favour of the wolves.

These results suggest that once the wolves are close to the flock, it is very hard for the dogs to protect all sheep: wolves either disturbed the flock, or wounded or killed at least one individual. These results contradict our prediction that livestock guarding dogs should remain in the immediate surrounding of the flock to protect it. Rather, our results suggest that while the proximity of the dogs to the flock may enable the dogs to intervene quickly in case of disturbance, it does not allow the dogs to prevent an attack. For this reason, to improve flock protection, we recommend that a livestock guarding dog group be made up of both dogs that remain in the immediate vicinity of the flock to prevent direct interactions between wolves and the flock (Allen et al. 2017) and dogs that move in a wider radius (ca. 300 m but up to 1,000 m depending on local conditions) around the flock (van Bommel & Johnson 2012, 2014b), especially when the flock is moving freely on pasture. Our recommendation is further supported by our finding that half of the interactions between livestock guarding dogs and wolves occurred at a distance greater than 300 m from the flock. Better sheep protection at our study sites thus relies in part on maintaining a buffer zone that will require wolves to confront livestock guarding dogs on two different occasions before being able to reach the flock.

Therefore, we propose that livestock guarding dogs' attentiveness and the bond between dogs and the flock should not be considered solely on the basis of proximity between dogs and sheep (Coppinger et al. 1983, Lorenz & Coppinger 1986). Rather, we suggest that the concept of a sensory bond between livestock guarding dogs and the flock be investigated. As long as the dogs can see, hear and/or smell the flock they are guarding, we may hypothesize that they are in contact with the flock and able to react to its behaviour. Thus, livestock guarding dogs that walk at a distance from the flock should not necessarily be considered to be wandering, as long as they keep in sensory contact with the flock they are guarding. The sensory distance between a dog and its flock depends on various factors such as terrain topography and weather. Therefore, sensory distance will vary with environmental conditions and should take into account the specific features of each summer pasture or grazing area. These two proposed circles of protection (i.e. inner circle with the flock and larger circle further away from the flock) should reinforce the overall effectiveness of dogs' guarding behaviour. The notion of sensory bonding is complex and would require more in-depth research before being implemented widely. It would also need to be adapted to the laws of each country where livestock guarding dogs are used, particularly with regard to public safety (van Bommel & Johnson 2014b). Indeed, there are records of livestock farmers being prosecuted and fined because their livestock guarding dogs had bitten hikers in France (Linder & Durand 2001). In one case, a livestock farmer was even given a suspended jail sentence (J.-M. Landry, pers.

observ.). This happens in part because pastoral systems are now multi-use systems where other users practice their hobby often without being aware of or having experience with large working dogs. This is the first time in their history that livestock guarding dogs have to work in highly touristic areas like the French Alps and that represent a real challenge for their owners and trainers. Raising awareness among the other users of pastoral areas will thus be crucial for implementing this strategy successfully. Similarly, communicating with local authorities about the role livestock guarding dogs play in the maintenance of pastoral activities in large carnivore areas is important, as local authorities have sometimes banned livestock guarding dogs from their communities, especially during the winter months, when livestock guarding dogs need to be confined, often close to human settlements (Gehring et al. 2010).

The particular case of carcasses

Although livestock guarding dogs are trained to protect livestock, our study highlights the high stakes that carcasses represent for both livestock guarding dogs and wolves. Feeding livestock guarding dogs with dead sheep is a common practice in pastoral systems in many countries, including in the French Alps (J.-M. Landry, pers. observ.). Scavenging behaviour, both on wild and domestic animals, has been observed in livestock guarding dogs on African farmland (van Vliet 2011, Whitehouse-Tedd et al. 2020) and when they have the opportunity, livestock guarding dogs can act as predators (Green et al. 1984, Timm & Schmidtz 1989, Marker et al. 2005a, b, Potgieter et al. 2013, 2016). The presence of carcasses on pastoral units might divert livestock guarding dogs' attention from the flock itself. More research on the impacts of carcasses on livestock guarding dogs' and wolves' behaviour would be interesting but would probably offer few possibilities for management as it is unlikely that livestock owners/shepherds would be able to move carcasses out of the reach of wolves on rugged alpine terrain.

Conclusion

By being at the interface between behavioural ecology, large carnivore conservation and livestock husbandry, our study focuses on an important and timely subject as more and more farmers need to protect their flocks against recolonizing protected carnivores, especially wolves. We show that although livestock guarding dogs have been successfully used in the southern French Alps, the general lack of data on how they interact with wolves has prevented improvement of their use in protecting livestock. The use of thermal imagery offered novel insights into the nocturnal relationships between livestock guarding dogs and their wild ancestors, and advanced our understanding of their coupled behaviour in a human-dominated landscape. Despite the presence of livestock guarding dogs, wolves were observed frequently in the pastoral system, which forms part of their home range. Yet, wolves did not always show an interest in the flock with which they shared the landscape. Although our study remained exploratory, some factors such as the gregariousness of the sheep, the presence and number of livestock guarding dogs, their proximity to the flock, and ability to interact with wolves could be used to improve livestock protection. The use of livestock guarding dogs comes at an additional cost and work load to farmers (Gehring et al. 2010). A better understanding of how to make the most of their presence to protect sheep will ensure that they remain an asset to farmers and shepherds.

Our results indicate that interactions between livestock guarding dogs and wolves are made up of a complex suite of behaviours that are not yet fully understood. The main challenge in understanding these interactions is that many components are likely to play a role in the process and its outcome, from ecological mechanisms (e.g. habitat structure, dog/wolf pack constitution) to behavioural (e.g. dogs' and wolves' behaviour and personalities, flock response to the canids' behaviour) and socio-historical aspects (e.g. livestock husbandry practices and farmers' experiences in a given region). Therefore, our results must be considered with caution outside the territories studied. As Lescureux & Linnell (2014) pointed out, the relationships between the two canids challenge our perceptions of the wild and the domestic. The frontier between these two concepts is more dynamic and subtle than we often appreciate. Further research on wolf behaviour on pasture, and their interactions with livestock protection methods, notably livestock guarding dogs, must accommodate this complex and ambiguous reality to foster a shared landscape where human activities and large carnivores can coexist.

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Supplementary online material

Table S1. Characteristics of the seven less intensively-monitored mountainous extensive-grazing units in and around the Mercantour National Park (M3-M7), on the Canjuers Plateau (C4) and in the Drôme (D1), France (https://www.ivb.cz/wp-content/uploads/JVB-vol.-69-3-2020-LandryJ.-M.-et-al.-Table-S1-1.docx).

Table S2. Details of the context in which physical fights (n = 9) occurred during interactions between livestock guarding dogs and wolves on pastoral units in the southern Alps, France (https://www.ivb.cz/wp-content/uploads/JVB-vol.-69-3-2020-LandryJ.-M.-et-al.-Table-S2.docx).