How leadership could be used to manage domestic and wild ungulate herds

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Abstract – In increasingly anthropized landscapes, it is essential to understand animal behaviour, and especially the movement patterns of domestic and wild species to ensure their management and conservation. More specifically, cohabitation between human populations and wildlife could be improved through the study of habitat use by groups of animals in terms of decision-making processes and leadership phenomena. Landscape anthropization particularly affects ungulates due to the increasing rarity of available territories for the grazing of domestic herds or the reintroduction of wild ones. To avoid damage to agricultural and private land, most herbivores are managed by herders, or contained in enclosed areas. Although this conventional management method is efficient, fences are costly and restrictive and contribute to the loss of genetic diversity by isolating other wild animal populations. A new system of herd management would be to replace conventional fences with virtual fencing systems to manage species of interest. This innovative method consists of GPS systems with a warning and punishing device attached to the animal that is triggered when the animal approaches the virtual limits of allocated territory. The most consistent way to control a group using virtual fences would be to fit the device on the identified leaders, who influence overall group decisions. In ungulates, older dominant females are generally more likely to lead collective movements and be followed by other group members because of their greater knowledge of the surrounding environment, their higher physiological needs during calving and their numerous social relationships in the group. These individual characteristics make them key individuals in the organisation of social groups, so they could be targeted for the development of virtual fence systems and the management of wildlife and livestock.

Keywords: Ungulates; Herd; Collective movements; Leadership; Management; Virtual fences

1. Introduction

1.1. Humans and ungulates cohabitation

The study of animal behaviour is an essential research area for domestic species management and wildlife conservation (Anderson, 2001; Sutherland, 1998). More specifically, understanding group decision-making processes and how leadership emerges is a key tool in the prediction of how social animals take decisions, move collectively and use their territories (Ramos et al., 2018, 2015). Indeed, in agricultural landscapes or in protected areas, humans have to monitor and manage the movements of some animal groups, especially ungulates, to facilitate access to herds, prevent their predation, limit their impact on the surrounding vegetation (Sorensen et al., 2015) or warn neighbouring human communities of their presence (Coltrane and Sinnott, 2015). The sociality of domesticated species facilitates the maintenance of herd cohesion, making it easier to locate the groups in pastureland and coordinate movements such as transhumance (Butt et al., 2009). However, animals can raid crops and damage private land when free-ranging or wild groups approach human-dominated areas (Osborn and Parker, 2003; Treves et al., 2006). Animals can also represent a physical danger to people in situations such as collisions between animals and vehicles (Seiler, 2004). In this context, studies about social behaviours, group movements and leadership of ungulates are crucial to optimizing the cohabitation between wildlife and the humans that frequent the natural environment, whether for leisure or professional reasons.

1.2. Emergence of leadership in ungulates

Most ungulates are herbivorous. They therefore forage in patchy environments of non-mobile food items of variable nutritive quality (Senft et al., 1987). Usually, these patches are rather widely distributed and allow several individuals to feed at the same time without competition. There are high numbers of ungulates in groups, particularly when they are grazers living in open habitats and facing high predation pressure (Focardi and Paveri-Fontana, 1992). To meet all their needs, these species have to move from one patch to another while maintaining group cohesion to keep the advantage of number (Stutz et al., 2018): coordination and synchronisation will be the key elements of a successful collective movement. In ungulates, as in many other taxa, the propensity to initiate group movements can depend on several individual characteristics such as age (McComb et al., 2011, 2001), sex (Bourjade and Sueur, 2010; Ihl and Bowyer, 2011), dominance hierarchy (Krueger et al., 2014; Squires

and Daws, 1975), reproductive status (Fischhoff et al., 2007) and personality (Briard et al., 2015). Social relationships between group members are also central to the initiation of group movements (Ramseyer et al., 2009b). Indeed, an individual's social preferences for related and affiliated conspecifics can have a profound impact on group organisation during movements, for instance in terms of the ability to attract followers (Ramos et al., 2018; Sueur and Petit, 2008).

1.3. Individual and social mechanisms involved in leadership phenomena

Preferential associations between group members are observed in most ungulate species (Berry and Bercovitch, 2015; Green et al., 1989; Ramos et al., 2018; Reinhardt, 1983), leading to the conclusion that all individuals are different in terms of individual characteristics and that collective decision-making processes are the result of non-random interactions between individuals.

In dimorphic species, the larger size of males compared to females results in different energy requirements, food selection, predator avoidance strategies or activity budgets (Ruckstuhl, 2007; Ruckstuhl and Neuhaus, 2000). Because of these differences, males and females often live in segregated groups, except during the breeding season when the energetic imbalance between sexes is reduced due to calving (Ruckstuhl and Neuhaus, 2000). Segregation may also occur according to reproductive status, as pregnant and lactating females are more exposed to predators and have a higher energetic demand than non-pregnant and non-lactating females (Neuhaus and Ruckstuhl, 2002; Ruckstuhl, 2007). Combined with kinship ties and preferential associations that exist within a group, these inter-individual differences make some individuals more likely than others to initiate movements and be followed by their conspecifics (Ramos et al., 2018, 2015). It is therefore valuable to understand the typical profile of a leader capable of attracting followers and the role of social relationships, especially for herd management (Anderson, 2007; Butler et al., 2006).

1.4. Leadership patterns and herd management

Our modern ecosystems have reduced the number of available territories for the grazing or reintroduction of wild herds of herbivores. In human-dominated landscapes, conflicts and damage to agricultural and private land are avoided by mustering herbivores or erecting physical fences to prevent animals from entering or leaving a given area (Bishop-Hurley et al.,

2007; Butler et al., 2006). Although these conventional fences provide effective solutions as physical constraints, they are costly in terms of manual labour, installation and maintenance (Butler et al., 2006; Jouven et al., 2010; Lee et al., 2018). The static nature of fences means that they cannot be easily moved to adapt and optimize the areas available for the nutritional needs of livestock (Anderson, 2007, 2001; Butler et al., 2006; Rose, 1991). Moreover, fences negatively impact wildlife: they not only prevent the target species from crossing, but are an obstacle for all other wild species (Jouven et al., 2010). In this respect, they contribute to the isolation of wild animal populations and all ensuing problems, such as loss of genetic diversity (Hayward and Kerley, 2009).

A new way of rethinking herd management is to dispense with traditional fences by developing virtual ones. This appealing tool consists of a GPS system coupled with a warning and punishing device attached to the animal via a neckband (Anderson, 2007; Jouven et al., 2010; Quigley et al., 1990). Using GPS technology and satellite to monitor animal movement and behavior, the device is activated when the equipped animal tries to cross the limits of the allocated territory (Lee and Campbell, 2021). In this case, a warning signal, followed by a negative stimulus if the individual proceeds across the virtual barriers, is thus delivered and generates the retreat of the animal from the unauthorised area (Anderson, 2007; Quigley et al., 1990). To be effective and ethically acceptable, this presupposes that the animal can associate the warning signal with their approach to the virtual barriers and learn to respond positively to the warning stimulus alone in order to avoid receiving the negative stimulus that follows, namely an electric shock (Campbell et al., 2020; Lee et al., 2009; Marini et al., 2018a). Thus, for a successful learning process, the virtual fences system must be predictable and controllable for the animal (Lee et al., 2018, 2009). This is in essence very similar to the principle of standard electric fences and presents the advantage of avoiding the collateral damages of other fencing options (entanglement in wires, cuts...).

According to several authors (Anderson, 2007; Keshavarzi et al., 2020; Ramos et al., 2018), one interesting strategy for the use of virtual fences to control a group, without equipping all individuals, would be to fit the GPS system on well-identified leaders and take into account the phenomena of social facilitation. The analysis of these behavioural processes therefore appears to be potentially useful for the management of herd movements in both pastoral and wild environments.

This review seeks to clarify the various processes underlying the collective movements of ungulates and will specify how this knowledge can play a role in the management of wild and domesticated ungulate herds. Finally, we will outline future avenues of research that can facilitate a reduction of human-wildlife conflicts.

2. Processes underlying collective movements in ungulates

2.1. The pre-departure period: when and where are we going?

Moving together is not an easy task, especially in large groups. A decision must be made as to the time of departure and the destination, but all individuals may not be ready to leave at the same time and mutually exclusive choices about direction can emerge (Bourjade and Sueur, 2010; Conradt and List, 2009; Petit and Bon, 2010). To preserve social cohesion and avoid conflicts of interest, it is therefore necessary to make compromises and reach a consensus (Conradt and Roper, 2010, 2005; Sumpter and Pratt, 2009). In some species, this is achieved through the expression of typical behaviours before the departure (Petit and Bon, 2010; Prins, 1996; Ramseyer et al., 2009a). Group members show their motivation to move through these behaviours (Table 1), called “intention movements”, “notifying behaviours” or “preliminary behaviours” (Bourjade et al., 2009; Petit and Bon, 2010; Ramseyer et al., 2009b). Ramseyer et al. (2009a) showed that activity, and particularly the frequency of steps and head movements, increased 30 minutes before departure in a flock of domestic sheep (*Ovis aries*). Similar results have been obtained in group departures of cattle [*Bos taurus*, (Ramseyer et al., 2009c)]. In Przewalski horses (*Equus ferus przewalskii*), individuals move away from the core of the group and thus indicate to counterparts their desire to change location (Bourjade et al., 2009; Bourjade and Sueur, 2010). Feral horses (*Equus ferus caballus*) and African buffalos (*Syncerus caffer*) tend to urinate and defecate more, and more often, before the triggering of a new group movement, making the time of departure predictable (Feist and McCullough, 1976).

Some of these behaviours express individual preferences for an alternative and can be considered as votes (Pennisi and Giallongo, 2018). A democratic process based on the relative number of individuals supporting each alternative can emerge during decision making (Conradt and Roper, 2007; List, 2004). Prins (1996) showed that African buffalo cows stood up just before a collective movement and oriented their body in the direction of their choice, keeping their head raised. The final decision about the direction of the departure took the

voters' opinions into account (Prins, 1996). A similar process has been observed in European bison [*Bison bonasus* (Ramos et al., 2015)], Przewalski horses (Bourjade et al., 2009; Bourjade and Sueur, 2010), and domestic sheep and cattle (Ramseyer et al., 2009a, 2009c), but not in goats [*Capra aegagrus hircus* (Sankey et al., 2021)]. Individuals who move first increase the probability of being followed by others when they take the collective choice into account (Petit and Bon, 2010; Ramseyer et al., 2009a, 2009c). For instance, the number of followers is higher in cattle and sheep if the direction of group movement has been chosen by the majority of individuals (Ramseyer et al., 2009a, 2009c). In European bison, the more individuals are oriented in the chosen direction before departure, the larger the number of participants will be (Ramos et al., 2015). However, the existence of a pre-departure period can also slow down the process of following, as observed in horses (Bourjade et al., 2009; Bourjade and Sueur, 2010). Indeed, if group members face in different directions before the departure of the first horse, it can be difficult for the group to reach a consensus while remaining cohesive (Bourjade et al., 2009; Bourjade and Sueur, 2010). Although this context causes the group to split in some species (Conradt and Roper, 2010; Ruckstuhl, 2007), horses seem to resolve the motivational conflict by taking more time to reach a consensus about which direction they will decide to take (Bourjade et al., 2009; Bourjade and Sueur, 2010).

Group size may have an important effect on these collective processes. More particularly, the higher the group size, the more difficult to communicate globally and reach a consensus with individuals of different needs. In this context, the probability to observe group fissions also increases (Couzin and Krause, 2003; Petit and Bon, 2010; Sueur et al., 2011).

Whether or not an individual takes the behaviours of its counterparts into account and adapts its own behaviour before moving may be decisive for the success of a collective movement (success expressed as the percentage of group members participating in the movement). Communication, through the information exchanged during the pre-departure period, is therefore at the core of social cohesion when the group gets under way (Petit and Bon, 2010). Certain individuals attract more counterparts than others and thus become influential leaders.

2.2. Profiling potential leaders

The term "leader" is often used to describe an individual with natural and disproportionate influence within the group, particularly by attracting other group members to him or her (Petit

and Bon, 2010). In the context of collective movements, leadership is the probability of an individual triggering the movement of others through its own movement (Dumont et al., 2005; King, 2010; Kummer, 1967; Lamprecht, 1992). However, the decision to move is rarely caused by one despotic individual (Lusseau and Conradt, 2009). The consensus is, indeed, generally shared (Conradt and Roper, 2005) and the initiation of movement can be triggered by several individuals, depending on the social and environmental context (Bourjade and Sueur, 2010; Ramos et al., 2016; Ramseier et al., 2009b). External observers often presume that the leaders have a specific social role, *i.e.* social leadership, and influence their peers by their age, sex or their dominance rank (Petit and Bon, 2010; Pillot et al., 2010).

Adult females are the individuals that initiate the most movements in matriarchal societies, as observed muskoxen, *Ovibos moschatus* (Ihl and Bowyer, 2011), American bison, *Bison bison* (McHugh, 1958) and European bison (Ramos et al., 2018, 2015). The common pattern often observed concerns old females in species such as Thornicroft's giraffe (*Giraffa camelopardalis thornicrofti*), in which they occupied leadership positions in 79% of cases (Berry and Bercovitch, 2015) or elephants (*Loxodonta africana*), in which the oldest female, the matriarch, always led group movements (McComb et al., 2011, 2001). Rowell (1991) also observed in sheep that the oldest ewe led the flocks in 82% of observations. Old individuals are always described as having a greater knowledge and experience of the environment, and would therefore be more likely to evaluate the risks and make ecologically relevant decisions for their group (McComb et al., 2011, 2001; Wittemyer et al., 2005). An old age can thus be a prerequisite to being a good leader in ungulates (Ramos et al., 2018; Reinhardt, 1983).

Hierarchical status can also play an important role in leadership distribution and following success (Sueur et al., 2018). In equids, which live in harem-type structures, the most frequent leaders are often the dominant individuals (Feist and McCullough, 1976; Krueger et al., 2014; Petit and Bon, 2010). For instance, in mountain and Hartmann zebras (*Equus zebra zebra* and *E. zebra hartmannae*), Klingel (1968) reported that the stallion, the most dominant individual, led its group to water sites and that the dominant mare then led when the group left. Several studies also showed that the order of individuals during the progression usually reflected the hierarchy of the group (Krueger et al., 2014; Tyler, 1972). In two domestic sheep breeds, there is a strong association between leadership and social rank, with the most dominant individuals positioning themselves at the front of the group movement (Squires and Daws, 1975). The influence of dominance on the leadership process is however far from being a rule in ungulates

(Reinhardt, 1983; Stewart and Scott, 1947). Beilharz & Mylrea (1963) noted that mixed breeding heifers of medium and low dominance ranks are positioned in front of dominant individuals during successively free and forced movements, thus showing that other parameters may be involved. In goats, the fact that an animal is dominant in a particular context does not help it to become a leader in group movement, and vice versa (Stewart and Scott, 1947). The authors concluded that leadership and dominance are the result of two distinct learning processes (Stewart and Scott, 1947).

For an individual, initiating a group movement could have a physiological basis (Petit and Bon, 2010; Sueur et al., 2013). Indeed, animals are forced to move to meet their nutritional needs, but the inter-individual differences make some individuals more likely to seek a change in location, and particularly those that have greater food requirements. The hypothesis that nutritional state is one of the main factors explaining leadership is supported by a model developed by Rands et al. (2008), who argued that an individual can be a leader without possessing any specific characteristic except its energetic reserve level. Moreover, these authors state that although a leader can emerge from a group of identical individuals (Rands et al., 2003), a difference in metabolism between them makes this event even more likely (Rands et al., 2008). In plains zebras (*Equus burchellii*) for example, lactating females trigger the movements of their harem more frequently than other individuals do, and their water and protein needs are substantially higher than those of their conspecifics (Fischhoff et al., 2007). By leading the group, lactating females are ensured priority access to water, a valuable contribution for milk production and foal survival (Fischhoff et al., 2007).

Leadership can also sometimes be affected by stress level, which is measured by the circulating level of glucocorticoid hormones. Glucocorticoid excretion increased in the alpha stallion when the enclosure of a group of Przewalski horses increased in size, and the stallion was more frequently observed at the front during group movements (Wolter et al., 2014); in a less stressful context, the alpha stallion is often at the rear (Feist and McCullough, 1976; Berger, 1977).

Personality differences can also be involved and affect whether individuals become initiators or followers. In a study of domestic horses, Briard et al. (2015) showed that bold individuals initiated movements more often than shy individuals, and positioned themselves preferentially at the front of the moving group. The authors' hypothesis is that bolder animals are more explorative and less anxious than others and therefore cope better with the

uncertainty of changing location. Their ability to initiate a collective movement could thus depend on their capacity to leave and be separated from their conspecifics.

Two models (Conradt et al., 2009; Lamprecht, 1996) show that the most socially indifferent individual is more likely than others to initiate group movements. The influence of personality has also been observed in other ungulate species such as sheep, in which shy individuals remained close to their conspecifics when grazing, whilst bold individuals grazed further away (Michelena et al., 2010; Sibbald et al., 2009).

2.3. Is social network important for leadership?

Initiating a movement is one thing, but being followed is another. Besides the influence of individual characteristics on the initiation phase and the following process, being able to attract followers also seems to be related to the social links an individual has with its conspecifics (Bode et al., 2011a; Ramos et al., 2018). Links can take many forms, including the parental link. It is known to be very strong in ungulates, often extending into adulthood (Le Pendu et al., 1995; Reinhardt, 1980; Tulloch, 1979; Tyler, 1972). Thus, it is not surprising to observe adult individuals following and staying close to their mothers during collective movements, as reported in muskoxen (Ihl and Bowyer, 2011) and zebu [*Bos taurus indicus* (Reinhardt and Reinhardt, 1981)]. In equines, females are especially observed to be followed by their foals, walking in order according to their age: the youngest is positioned immediately behind the mother and then the older offspring (Klingel, 1977; Tyler, 1972). Maternal bonds can thus explain why in some cases, adult females have a greater ability to attract followers (*i.e.*, a better leadership success) compared to males: their progeny are automatic followers (Green et al., 1989). Conversely, by moving away from their mother to explore, calves can also have an important role in the triggering of movements. This has been observed in European bison; juveniles that moved away from their group were systematically followed by their mother, thus resulting in a cascading reaction of the whole group through a mimetic process (Ramos et al., 2015).

In addition to the mother-young bond, the literature also describes how individuals follow close relatives during collective movements. For instance, adult female giraffes have been observed following their eldest sibling (Berry and Bercovitch, 2015). Furthermore, kinship influences the composition of giraffe herds because they often consist of matrilineal relatives (Berry and Bercovitch, 2015). The same is true for elephants (Archie et al., 2006), zebras

(Reinhardt and Reinhardt, 1981) and water buffalo [*Bubalus bubalis* (Tulloch, 1979)]. In pigs (*Sus scrofa domesticus*), the individuals with the highest number of relatives are more prone to be leaders than other group members (Meese and Ewbank, 1973). Social preferences for kin individuals thus seems to shape group organisation and following success, which is also true for affiliative bonds (Bode et al., 2011a). Indeed, in many ungulates, individuals that are linked by friendly bonds will tend to follow each other during spontaneous group movements [e.g. cattle and sheep (Della-Rossa et al., 2013; Ramseyer et al., 2009b), and horses (Wells and von Goldschmidt-Rothschild, 1979; Briard et al., 2015)]. Boissy and Dumont (2002) showed that individual ewe lambs walked away from the group towards preferred food patches more easily when they were accompanied by familiar conspecifics. In a Y-maze test, Murray et al. (2013) showed that donkeys (*Equus asinus*) chose to go towards their preferred companion rather than a familiar or unfamiliar individual. In the hippopotamus (*Hippopotamus amphibius*), rafting females associate more with kin and their closest conspecifics (Blowers et al., 2010). All these observations suggest that “friendship” preferences can have a profound impact on group organisation and collective movements (Bode et al., 2011b, 2011a; Sueur et al., 2018). In particular, they seem to provide social support for individuals (Boissy and Dumont, 2002) and can confer several advantages such as the cooperative defence of calves or resources, parenting assistance and high group social cohesion (Lazo, 1994; Archie et al., 2006).

Affinities can also be driven by inter-individual similarities in age class, dominance rank or personality. Briard et al. (2015) showed that horses with a similar hierarchical rank and boldness level tend to follow each other during the joining process. In matriarchal societies, and in a large number of ungulate species, males are more independent than females; whereas young females stay in the maternal group, males leave it shortly after weaning to form small same-sex peer groups before evolving solitarily into adulthood (Appleby, 1983; Bon and Campan, 1996; Ruckstuhl and Neuhaus, 2000). These social tendencies and this greater independence of males could therefore explain why they have fewer followers than females do when they move away from mixed-sex groups: their bonds are weaker and restricted because of their early selective association preferences with each other (Ihl and Bowyer, 2011; Ramos et al., 2015). In contrast, staying in the maternal group gives young females the opportunity to create more varied and strong relationships. These females thus become more likely to rally others during collective movements (Box and Gibson, 1999).

3. The usefulness of leadership in herd management.

As humans are increasingly monopolising land use through intensive agriculture, road networks and urban expansion, it is increasingly difficult to obtain a good cohabitation with domestic and wild herds of animals. The leadership mechanisms described above may play a central role in the development of technical tools such as virtual fences (Anderson, 2007, 2001; Marini et al., 2020), which could reduce conflicts over space use between humans and ungulates. As described earlier, the system consists of a GPS system attached to the animal that first triggers a warning sound when it approaches the virtual boundaries of the territory, immediately followed by a negative stimulus (often an electric shock) if the individual proceeds across (Anderson, 2007; Jouven et al., 2010; Quigley et al., 1990). This negative stimulus then generates the stopping or the retreat of the individual (Anderson, 2007; Lee et al., 2009; Quigley et al., 1990). From this, the animal will learn to associate the diffusion of the warning sound alone with the appropriate behaviour (namely the turning back) to avoid the shock which follows (Lee et al., 2018).

One important precondition for the use of virtual fences is that animals associate the audio stimulus with spatial restrictions (Butler et al., 2006; Lee et al., 2018). Tiedemann et al. (1999) observed that heifers learned the location of the exclusion area after just two trials. In another study, even if there were no obvious visual cues for animals, the authors showed that cattle had developed spatial awareness after the third trial (Bishop-Hurley et al., 2007). In sheep, Marini et al. (2018a) showed that animals learn to respond to the audio cue after about eight interactions. However, recent studies have shown that both cattle and sheep are actually learning to respond to the audio cue and not the location in which it was given (Campbell et al., 2020, 2017; Lee and Campbell, 2021; Marini et al., 2018a). For instance, Campbell et al. (2017) revealed that heifers adapted almost instantly each time that virtual fences were successively moved, meaning that the emission of the warning signal had become sufficient to prevent them from going further. In sheep, when the virtual fences are removed, the animals hurry to cross to reach the part of their pasture which was previously prohibited (Marini et al., 2018a).

However, the speed at which fitted animals appear to learn the relationship between their movements and the following consequences is counterbalanced by a significant inter-individual variability, both in cattle (Campbell et al., 2020, 2019) and sheep (Marini et al., 2018b). In the worst case, some individuals can remain motionless during the electric stimulus,

or try to cross into the exclusion areas despite the discomfort (Fay et al., 1989; Jouven et al., 2010; Quigley et al., 1990). The welfare of animals and effectiveness of the virtual fences in retaining herd can be particularly questioned in case of technical failures, or a serious disturbance such as a sudden noise or a predator attack (Jouven et al., 2010). In this context, it is thus not possible to exclude the risk of injuries or chronic stress (Anderson, 2001). In Lee et al. (2009) study, the use of an audio cue to warn animals of future electric shocks precisely reduced the number of electric shocks received, compared to a punishment system alone. Moreover, if an animal run into the exclusion zone, the *Agersens* system developed from the same study paper resets the boundary in front of it; the system only provides supplementary signals if the animal moves further into the exclusion zone but no more signals will be received if the animal moves back to the inclusion zone. These results have important implications for the development of an adaptive and welfare-friendly technology, especially by using non-aversive conditioning stimuli. Nevertheless, consideration of physiological indicators of stress (heart rate, cortisol, core body temperature etc.), behavioural responses, cognition (associative and social learning) etc. are all necessary to evaluate the harmlessness of a new technology (Lee and Campbell, 2021).

Finally, the other aspect relating to the security of such a system is the absence of physical fences which could, for instance, facilitate livestock thefts (Jouven et al., 2010) or damage such as car collision in case of escape. According to Lee et al. (2021), as the virtual fencing is not 100% effective at containing herds, it should only be used for internal fencing to reduce these risks. Further research is needed before virtual fencing replace physical ones and becomes a reality.

Although it is easily conceivable to equip domestic herds, follow their learning and ensure the maintenance of installations, it seems much more difficult to implement such a technology for wild ungulate species, because it requires to localize and anesthetize animals, to monitor them in limiting environmental conditions while ensuring battery life and animal welfare.

A project was tested in 2009 on a European bison herd chosen to be reintroduced in the Rothaargebirge region in Germany (Rewilding Europe, 2014; von Mirko and Lindner, 2008). Although bounded by an existing game fence to the South, bison migration was supposed to be prevented in the North by a virtual fence device consisting of buried induction loops and collars worn by the animals that couple an audio-warning system with an electric receptor (Kleinlogel, 2009). Despite encouraging results, the level of experience and knowledge of the

device was not yet sufficient to pursue further trials on this species. Several other factors may have ended the experience prematurely such as the acceptance of the population to cohabit with bison without physical fences between them, and the cost of the equipment and maintenance.

However, it may not be necessary to equip every animal with a collar to control the entire group, since ungulate species generally have a strong herd instinct. Indeed, several studies confirm the importance of leaders' behaviours in the responses of the other group members. In livestock, Tiedemann et al. (1999) showed that when the electric device of leaders became inactive, the leaders moved to the exclusion zone and were followed by other fitted individuals that endured the audio-electrical shock to join them (Tiedemann et al., 1999). Fay et al. (1989) concluded that training the most dominant goats in a group might permit herd containment with a minimum number of equipped individuals. Sheep can also be controlled by training a small number of individuals to avoid certain areas (Lynch et al., 1992). In particular, Marini et al. (2020) have shown that, for a short period, controlling two-thirds of a flock was equally as effective as equipping all individuals while controlling one-third of a flock is not enough. Keshavarzi et al. (2020) prefer to talk about social facilitation influence, as there is no exclusive herd leadership in their studied group of Angus cattle. In this case, the leadership behaviour applied to the system of virtual barriers seems to be difficult to envisage to contain an entire herd (Keshavarzi et al., 2020). This is especially true for species with large groups and a "fission-fusion" dynamics (Ramos et al., 2018, 2015). It thus appears interesting to better understand social behaviours in ungulates, more specifically by identifying the profiles of individuals that potentially influence the movements and reactions of the others, before considering virtual fence, applied to the leadership pattern, as an innovative management tool. In ungulates, especially for matriarchal societies, it seems that old females, which are also often the most dominant individuals, are good candidates given their experience and their strong social links with others (McComb et al., 2011; Ramos et al., 2018; Rowell, 1991).

4. Conclusion and future research framework

There has been increasing interest in leadership and the influence of social network influences in animal species over recent years. This research subject is not only interesting from an evolutionary point of view, but also from a mechanistic perspective, for example to

416 better understand how animals communicate and find consensus within groups. This
417 challenge is especially evident in ungulates, and particularly wild populations, which have to
418 travel long distances between feeding sites and water points while avoiding predators. In this
419 respect, ungulates are a good model for the study of leadership mechanisms. Moreover, the
420 potential of leadership studies in terms of herd management strategies is evident given the
421 omnipresence of ungulates in the domestication process and animal farming. Applying our
422 leadership findings to this domestication process will improve the management of livestock
423 that range in large wild spaces.

424 Current studies on virtual fences for ungulates are currently at the experimental stage and
425 seek to improve and measure the feasibility of such management methods, especially for large
426 groups (Campbell et al., 2019). The study of leadership and social facilitation for application in
427 herd management, and the understanding of cognitive processes behind, are still in their
428 infancy and should be developed further (Campbell et al., 2019; Keshavarzi et al., 2020). A
429 comprehensive understanding of group decisions in ungulates could allow us to predict which
430 individuals could have influence in a given herd, which would be of direct benefit to pastoral
431 and wildlife conservation programs in terms of management practices (Ramos et al., 2015).
432 Thus, many questions remain to be answered: are there clearly identifiable leaders and if so,
433 what their main characteristics are? how many individuals could be equipped in a herd to
434 contain it efficiently? Is it necessary to systematically train animals with the device, and if so,
435 how can it actually be implemented in current wild populations given the technical
436 constraints? Can people be convinced that fences between people and animals could be,
437 ultimately, safely removed? This last question also raises the need to study the interactions
438 between humans and herds to ensure security in the case of an encounter without physical
439 fences. The information and knowledge obtained from these different avenues of research
440 would allow better management and thus better cohabitation between humans and wildlife,
441 leading to a significant reduction in conflicts.

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Table 1. Notifying behaviours during pre-departure period and characteristics influencing initiation of movements for several studied ungulate species. The cross symbol indicates what it is reported in the literature about the presence of pre-departure behaviours (increase of activity, increase of excretion or expression of “voting behaviours”) and the influence of individual characteristics (age, sex, dominance, physiological state and personality) on the propensity to initiate collective movements.

Family	Species	Pre-departure			Initiation					Article
		Activity	Excretion	Voting behaviours	Age	Sex	Dominance	Physiological state	Personality	
Equidae	<i>Equus caballus</i>	X	X	X			X	X	X	(Tyler, 1972) (Feist and McCullough, 1976) (Berger, 1977) (Krueger et al., 2014) (Briard et al., 2015)
	<i>Equus zebra zebra</i>						X			(Klingel, 1968)
	<i>Equus zebra hartmannae</i>						X			(Klingel, 1968)
	<i>Equus ferus przewalskii</i>			X	X			X		(Bourjade et al., 2009) (Bourjade and Sueur, 2010) (Wolter et al., 2014)
	<i>Equus burchellii</i>							X		(Fischhoff et al., 2007)

Table 1. (cont'd)

Family	Species	Pre-departure			Initiation					Article
		Activity	Excretion	Voting behaviours	Age	Sex	Dominance	Physiological state	Personality	
Ovidae	<i>Ovis aries</i>	X		X	X		X		X	(Rowell, 1991) (Squires and Daws, 1975) (Ramseyer et al., 2009a) (Sibbald et al., 2009) (Michelena et al., 2010)
Bovidae	<i>Syncerus caffer</i>		X	X		X				(Prins, 1996)
	<i>Bison bison</i>				X	X				(McHugh, 1958)
	<i>Bison bonasus</i>			X	X	X				(Ramos et al., 2015) (Ramos et al., 2018)
	<i>Bos indicus</i>					X				(Reinhardt, 1983)
	<i>Bos taurus</i>	X		X	X		X			(Beilharz and Mylrea, 1963) (Dumont et al., 2005) (Ramseyer et al., 2009c) (Sueur et al., 2018)
Caprinae	<i>Ovibos moschatus</i>				X	X				(Ihl and Bowyer, 2011)
Giraffidae	<i>Giraffa camelopardalis thornicrofti</i>				X	X				(Berry and Bercovitch, 2015)