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

2

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10

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

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

34 **1. Introduction**

35 1.1. Humans and ungulates cohabitation

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

54

55 1.2. Emergence of leadership in ungulates

56 Most ungulates are herbivorous. They therefore forage in patchy environments of non-
57 mobile food items of variable nutritive quality (Senft et al., 1987). Usually, these patches are
58 rather widely distributed and allow several individuals to feed at the same time without
59 competition. There are high numbers of ungulates in groups, particularly when they are
60 grazers living in open habitats and facing high predation pressure (Focardi and Paveri-
61 Fontana, 1992). To meet all their needs, these species have to move from one patch to
62 another while maintaining group cohesion to keep the advantage of number (Stutz et al.,
63 2018): coordination and synchronisation will be the key elements of a successful collective
64 movement.

65 In ungulates, as in many other taxa, the propensity to initiate group movements can depend
66 on several individual characteristics such as age (McComb et al., 2011, 2001), sex (Bourjade
67 and Sueur, 2010; Ihl and Bowyer, 2011), dominance hierarchy (Krueger et al., 2014; Squires
68 and Daws, 1975), reproductive status (Fischhoff et al., 2007) and personality (Briard et al.,
69 2015). Social relationships between group members are also central to the initiation of
70 group movements (Ramseyer et al., 2009b). Indeed, an individual's social preferences for
71 related and affiliated conspecifics can have a profound impact on group organisation during
72 movements, for instance in terms of the ability to attract followers (Ramos et al., 2018;
73 Sueur and Petit, 2008).

74

75 1.3. Individual and social mechanisms involved in leadership phenomena

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

81 In dimorphic species, the larger size of males compared to females results in different
82 energy requirements, food selection, predator avoidance strategies or activity budgets
83 (Ruckstuhl, 2007; Ruckstuhl and Neuhaus, 2000). Because of these differences, males and
84 females often live in segregated groups, except during the breeding season when the
85 energetic imbalance between sexes is reduced due to calving (Ruckstuhl and Neuhaus,
86 2000). Segregation may also occur according to reproductive status, as pregnant and
87 lactating females are more exposed to predators and have a higher energetic demand than
88 non-pregnant and non-lactating females (Neuhaus and Ruckstuhl, 2002; Ruckstuhl, 2007).
89 Combined with kinship ties and preferential associations that exist within a group, these
90 inter-individual differences make some individuals more likely than others to initiate
91 movements and be followed by their conspecifics (Ramos et al., 2018, 2015). It is therefore
92 valuable to understand the typical profile of a leader capable of attracting followers and the
93 role of social relationships, especially for herd management (Anderson, 2007; Butler et al.,
94 2006).

95

96

1.4. Leadership patterns and herd management

97

98 Our modern ecosystems have reduced the number of available territories for the grazing
99 or reintroduction of wild herds of herbivores. In human-dominated landscapes, conflicts and
100 damage to agricultural and private land are avoided by mustering herbivores or erecting
101 physical fences to prevent animals from entering or leaving a given area (Bishop-Hurley et
102 al., 2007; Butler et al., 2006). Although these conventional fences provide effective solutions
103 as physical constraints, they are costly in terms of manual labour, installation and
104 maintenance (Butler et al., 2006; Jouven et al., 2010; Lee et al., 2018). The static nature of
105 fences means that they cannot be easily moved to adapt and optimize the areas available for
106 the nutritional needs of livestock (Anderson, 2007, 2001; Butler et al., 2006; Rose, 1991).
107 Moreover, fences negatively impact wildlife: they not only prevent the target species from
108 crossing, but are an obstacle for all other wild species (Jouven et al., 2010). In this respect,
109 they contribute to the isolation of wild animal populations and all ensuing problems, such as
110 loss of genetic diversity (Hayward and Kerley, 2009).

110

111 A new way of rethinking herd management is to dispense with traditional fences by
112 developing virtual ones. This appealing tool consists of a GPS system coupled with a warning
113 and punishing device attached to the animal via a neckband (Anderson, 2007; Jouven et al.,
114 2010; Quigley et al., 1990). Using GPS technology and satellite to monitor animal movement
115 and behavior, the device is activated when the equipped animal tries to cross the limits of
116 the allocated territory (Lee and Campbell, 2021). In this case, a warning signal, followed by a
117 negative stimulus if the individual proceeds across the virtual barriers, is thus delivered and
118 generates the retreat of the animal from the unauthorised area (Anderson, 2007; Quigley et
119 al., 1990). To be effective and ethically acceptable, this presupposes that the animal can
120 associate the warning signal with their approach to the virtual barriers and learn to respond
121 positively to the warning stimulus alone in order to avoid receiving the negative stimulus
122 that follows, namely an electric shock (Campbell et al., 2020; Lee et al., 2009; Marini et al.,
123 2018a). Thus, for a successful learning process, the virtual fences system must be predictable
124 and controllable for the animal (Lee et al., 2018, 2009). This is in essence very similar to the
125 principle of standard electric fences and presents the advantage of avoiding the collateral
126 damages of other fencing options (entanglement in wires, cuts...).

126

127 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

128 equipping all individuals, would be to fit the GPS system on well-identified leaders and take
129 into account the phenomena of social facilitation. The analysis of these behavioural
130 processes therefore appears to be potentially useful for the management of herd
131 movements in both pastoral and wild environments.

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

136

137 **2. Processes underlying collective movements in ungulates**

138 **2.1. The pre-departure period: when and where are we going?**

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

158 Some of these behaviours express individual preferences for an alternative and can be
159 considered as votes (Pennisi and Giallongo, 2018). A democratic process based on the

160 relative number of individuals supporting each alternative can emerge during decision
161 making (Conradt and Roper, 2007; List, 2004). Prins (1996) showed that African buffalo cows
162 stood up just before a collective movement and oriented their body in the direction of their
163 choice, keeping their head raised. The final decision about the direction of the departure
164 took the voters' opinions into account (Prins, 1996). A similar process has been observed in
165 European bison [*Bison bonasus* (Ramos et al., 2015)], Przewalski horses (Bourjade et al.,
166 2009; Bourjade and Sueur, 2010), and domestic sheep and cattle (Ramseyer et al., 2009a,
167 2009c), but not in goats [*Capra aegagrus hircus* (Sankey et al., 2021)]. Individuals who move
168 first increase the probability of being followed by others when they take the collective
169 choice into account (Petit and Bon, 2010; Ramseyer et al., 2009a, 2009c). For instance, the
170 number of followers is higher in cattle and sheep if the direction of group movement has
171 been chosen by the majority of individuals (Ramseyer et al., 2009a, 2009c). In European
172 bison, the more individuals are oriented in the chosen direction before departure, the larger
173 the number of participants will be (Ramos et al., 2015). However, the existence of a pre-
174 departure period can also slow down the process of following, as observed in horses
175 (Bourjade et al., 2009; Bourjade and Sueur, 2010). Indeed, if group members face in different
176 directions before the departure of the first horse, it can be difficult for the group to reach a
177 consensus while remaining cohesive (Bourjade et al., 2009; Bourjade and Sueur, 2010).
178 Although this context causes the group to split in some species (Conradt and Roper, 2010;
179 Ruckstuhl, 2007), horses seem to resolve the motivational conflict by taking more time to
180 reach a consensus about which direction they will decide to take (Bourjade et al., 2009;
181 Bourjade and Sueur, 2010).

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

186 Whether or not an individual takes the behaviours of its counterparts into account and
187 adapts its own behaviour before moving may be decisive for the success of a collective
188 movement (success expressed as the percentage of group members participating in the
189 movement). Communication, through the information exchanged during the pre-departure
190 period, is therefore at the core of social cohesion when the group gets under way (Petit and

191 Bon, 2010). Certain individuals attract more counterparts than others and thus become
192 influential leaders.

193

194 2.2. Profiling potential leaders

195 The term “leader” is often used to describe an individual with natural and
196 disproportionate influence within the group, particularly by attracting other group members
197 to him or her (Petit and Bon, 2010). In the context of collective movements, leadership is the
198 probability of an individual triggering the movement of others through its own movement
199 (Dumont et al., 2005; King, 2010; Kummer, 1967; Lamprecht, 1992). However, the decision
200 to move is rarely caused by one despotic individual (Lusseau and Conradt, 2009). The
201 consensus is, indeed, generally shared (Conradt and Roper, 2005) and the initiation of
202 movement can be triggered by several individuals, depending on the social and
203 environmental context (Bourjade and Sueur, 2010; Ramos et al., 2016; Ramseyer et al.,
204 2009b). External observers often presume that the leaders have a specific social role, *i.e.*
205 social leadership, and influence their peers by their age, sex or their dominance rank (Petit
206 and Bon, 2010; Pillot et al., 2010).

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

219 Hierarchical status can also play an important role in leadership distribution and
220 following success (Sueur et al., 2018). In equids, which live in harem-type structures, the
221 most frequent leaders are often the dominant individuals (Feist and McCullough, 1976;
222 Krueger et al., 2014; Petit and Bon, 2010). For instance, in mountain and Hartmann zebras

223 (*Equus zebra zebra* and *E. zebra hartmannae*), Klingel (1968) reported that the stallion, the
224 most dominant individual, led its group to water sites and that the dominant mare then led
225 when the group left. Several studies also showed that the order of individuals during the
226 progression usually reflected the hierarchy of the group (Krueger et al., 2014; Tyler, 1972). In
227 two domestic sheep breeds, there is a strong association between leadership and social
228 rank, with the most dominant individuals positioning themselves at the front of the group
229 movement (Squires and Daws, 1975). The influence of dominance on the leadership process
230 is however far from being a rule in ungulates (Reinhardt, 1983; Stewart and Scott, 1947).
231 Beilharz & Mylrea (1963) noted that mixed breeding heifers of medium and low dominance
232 ranks are positioned in front of dominant individuals during successively free and forced
233 movements, thus showing that other parameters may be involved. In goats, the fact that an
234 animal is dominant in a particular context does not help it to become a leader in group
235 movement, and vice versa (Stewart and Scott, 1947). The authors concluded that leadership
236 and dominance are the result of two distinct learning processes (Stewart and Scott, 1947).

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

251 Leadership can also sometimes be affected by stress level, which is measured by the
252 circulating level of glucocorticoid hormones. Glucocorticoid excretion increased in the alpha
253 stallion when the enclosure of a group of Przewalski horses increased in size, and the stallion
254 was more frequently observed at the front during group movements (Wolter et al., 2014); in

255 a less stressful context, the alpha stallion is often at the rear (Feist and McCullough, 1976;
256 Berger, 1977).

257 Personality differences can also be involved and affect whether individuals become
258 initiators or followers. In a study of domestic horses, Briard et al. (2015) showed that bold
259 individuals initiated movements more often than shy individuals, and positioned themselves
260 preferentially at the front of the moving group. The authors' hypothesis is that bolder
261 animals are more explorative and less anxious than others and therefore cope better with
262 the uncertainty of changing location. Their ability to initiate a collective movement could
263 thus depend on their capacity to leave and be separated from their conspecifics.

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

269

270 2.3. Is social network important for leadership?

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

287 systematically followed by their mother, thus resulting in a cascading reaction of the whole
288 group through a mimetic process (Ramos et al., 2015).

289 In addition to the mother-young bond, the literature also describes how individuals
290 follow close relatives during collective movements. For instance, adult female giraffes have
291 been observed following their eldest sibling (Berry and Bercovitch, 2015). Furthermore,
292 kinship influences the composition of giraffe herds because they often consist of matrilineal
293 relatives (Berry and Bercovitch, 2015). The same is true for elephants (Archie et al., 2006),
294 zebus (Reinhardt and Reinhardt, 1981) and water buffalo [*Bubalus bubalis* (Tulloch, 1979)].
295 In pigs (*Sus scrofa domesticus*), the individuals with the highest number of relatives are more
296 prone to be leaders than other group members (Meese and Ewbank, 1973). Social
297 preferences for kin individuals thus seems to shape group organisation and following
298 success, which is also true for affiliative bonds (Bode et al., 2011a). Indeed, in many
299 ungulates, individuals that are linked by friendly bonds will tend to follow each other during
300 spontaneous group movements [*e.g.* cattle and sheep (Della-Rossa et al., 2013; Ramseyer et
301 al., 2009b), and horses (Wells and von Goldschmidt-Rothschild, 1979; Briard et al., 2015)].
302 Boissy and Dumont (2002) showed that individual ewe lambs walked away from the group
303 towards preferred food patches more easily when they were accompanied by familiar
304 conspecifics. In a Y-maze test, Murray et al. (2013) showed that donkeys (*Equus asinus*)
305 chose to go towards their preferred companion rather than a familiar or unfamiliar
306 individual. In the hippopotamus (*Hippopotamus amphibius*), rafting females associate more
307 with kin and their closest conspecifics (Blowers et al., 2010). All these observations suggest
308 that “friendship” preferences can have a profound impact on group organisation and
309 collective movements (Bode et al., 2011b, 2011a; Sueur et al., 2018). In particular, they seem
310 to provide social support for individuals (Boissy and Dumont, 2002) and can confer several
311 advantages such as the cooperative defence of calves or resources, parenting assistance and
312 high group social cohesion (Lazo, 1994; Archie et al., 2006).

313 Affinities can also be driven by inter-individual similarities in age class, dominance rank
314 or personality. Briard et al. (2015) showed that horses with a similar hierarchical rank and
315 boldness level tend to follow each other during the joining process. In matriarchal societies,
316 and in a large number of ungulate species, males are more independent than females;
317 whereas young females stay in the maternal group, males leave it shortly after weaning to
318 form small same-sex peer groups before evolving solitarily into adulthood (Appleby, 1983;

319 Bon and Campan, 1996; Ruckstuhl and Neuhaus, 2000). These social tendencies and this
320 greater independence of males could therefore explain why they have fewer followers than
321 females do when they move away from mixed-sex groups: their bonds are weaker and
322 restricted because of their early selective association preferences with each other (Ihl and
323 Bowyer, 2011; Ramos et al., 2015). In contrast, staying in the maternal group gives young
324 females the opportunity to create more varied and strong relationships. These females thus
325 become more likely to rally others during collective movements (Box and Gibson, 1999).

326 **3. The usefulness of leadership in herd management.**

327 As humans are increasingly monopolising land use through intensive agriculture, road
328 networks and urban expansion, it is increasingly difficult to obtain a good cohabitation with
329 domestic and wild herds of animals. The leadership mechanisms described above may play a
330 central role in the development of technical tools such as virtual fences (Anderson, 2007,
331 2001; Marini et al., 2020), which could reduce conflicts over space use between humans and
332 ungulates. As described earlier, the system consists of a GPS system attached to the animal
333 that first triggers a warning sound when it approaches the virtual boundaries of the territory,
334 immediately followed by a negative stimulus (often an electric shock) if the individual
335 proceeds across (Anderson, 2007; Jouven et al., 2010; Quigley et al., 1990). This negative
336 stimulus then generates the stopping or the retreat of the individual (Anderson, 2007; Lee et
337 al., 2009; Quigley et al., 1990). From this, the animal will learn to associate the diffusion of
338 the warning sound alone with the appropriate behaviour (namely the turning back) to avoid
339 the shock which follows (Lee et al., 2018).

340 One important precondition for the use of virtual fences is that animals associate the
341 audio stimulus with spatial restrictions (Butler et al., 2006; Lee et al., 2018). Tiedemann et al.
342 (1999) observed that heifers learned the location of the exclusion area after just two trials.
343 In another study, even if there were no obvious visual cues for animals, the authors showed
344 that cattle had developed spatial awareness after the third trial (Bishop-Hurley et al., 2007).
345 In sheep, Marini et al. (2018a) showed that animals learn to respond to the audio cue after
346 about eight interactions. However, recent studies have shown that both cattle and sheep are
347 actually learning to respond to the audio cue and not the location in which it was given
348 (Campbell et al., 2020, 2017; Lee and Campbell, 2021; Marini et al., 2018a). For instance,
349 Campbell et al. (2017) revealed that heifers adapted almost instantly each time that virtual
350 fences were successively moved, meaning that the emission of the warning signal had

351 become sufficient to prevent them from going further. In sheep, when the virtual fences are
352 removed, the animals hurry to cross to reach the part of their pasture which was previously
353 prohibited (Marini et al., 2018a).

354 However, the speed at which fitted animals appear to learn the relationship between
355 their movements and the following consequences is counterbalanced by a significant inter-
356 individual variability, both in cattle (Campbell et al., 2020, 2019) and sheep (Marini et al.,
357 2018b). In the worst case, some individuals can remain motionless during the electric
358 stimulus, or try to cross into the exclusion areas despite the discomfort (Fay et al., 1989;
359 Jouven et al., 2010; Quigley et al., 1990). The welfare of animals and effectiveness of the
360 virtual fences in retaining herd can be particularly questioned in case of technical failures, or
361 a serious disturbance such as a sudden noise or a predator attack (Jouven et al., 2010). In
362 this context, it is thus not possible to exclude the risk of injuries or chronic stress (Anderson,
363 2001). In Lee et al. (2009) study, the use of an audio cue to warn animals of future electric
364 shocks precisely reduced the number of electric shocks received, compared to a punishment
365 system alone. Moreover, if an animal run into the exclusion zone, the *Agersens* system
366 developed from the same study paper resets the boundary in front of it; the system only
367 provides supplementary signals if the animal moves further into the exclusion zone but no
368 more signals will be received if the animal moves back to the inclusion zone. These results
369 have important implications for the development of an adaptive and welfare-friendly
370 technology, especially by using non-aversive conditioning stimuli. Nevertheless,
371 consideration of physiological indicators of stress (heart rate, cortisol, core body
372 temperature etc.), behavioural responses, cognition (associative and social learning) etc. are
373 all necessary to evaluate the harmlessness of a new technology (Lee and Campbell, 2021).

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

380 Although it is easily conceivable to equip domestic herds, follow their learning and
381 ensure the maintenance of installations, it seems much more difficult to implement such a
382 technology for wild ungulate species, because it requires to localize and anesthetize animals,

383 to monitor them in limiting environmental conditions while ensuring battery life and animal
384 welfare.

385 A project was tested in 2009 on a European bison herd chosen to be reintroduced in the
386 Rothaargebirge region in Germany (Rewilding Europe, 2014; von Mirko and Lindner, 2008).
387 Although bounded by an existing game fence to the South, bison migration was supposed to
388 be prevented in the North by a virtual fence device consisting of buried induction loops and
389 collars worn by the animals that couple an audio-warning system with an electric receptor
390 (Kleinlogel, 2009). Despite encouraging results, the level of experience and knowledge of the
391 device was not yet sufficient to pursue further trials on this species. Several other factors
392 may have ended the experience prematurely such as the acceptance of the population to
393 cohabit with bison without physical fences between them, and the cost of the equipment
394 and maintenance.

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

415 it seems that old females, which are also often the most dominant individuals, are good
416 candidates given their experience and their strong social links with others (McComb et al.,
417 2011; Ramos et al., 2018; Rowell, 1991).

418

419 **4. Conclusion and future research framework**

420 There has been increasing interest in leadership and the influence of social network
421 influences in animal species over recent years. This research subject is not only interesting
422 from an evolutionary point of view, but also from a mechanistic perspective, for example to
423 better understand how animals communicate and find consensus within groups. This
424 challenge is especially evident in ungulates, and particularly wild populations, which have to
425 travel long distances between feeding sites and water points while avoiding predators. In
426 this respect, ungulates are a good model for the study of leadership mechanisms. Moreover,
427 the potential of leadership studies in terms of herd management strategies is evident given
428 the omnipresence of ungulates in the domestication process and animal farming. Applying
429 our leadership findings to this domestication process will improve the management of
430 livestock that range in large wild spaces.

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

447 different avenues of research would allow better management and thus better cohabitation
448 between humans and wildlife, 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)