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1 **Impact of interspecific hybridization between sika and red deer**  
2 **on phenotypic traits of the newborn and establishment of mother-young relationships**

3

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24 **ABSTRACT**

25 Pre-existing geographical barriers between species have been removed notably by humans,  
26 leading to possible hybridization between previously isolated species. Inter-species  
27 hybridization has been studied at different levels but the mother-young relationship, that is  
28 crucial for young survival, has not so far been investigated in wild mammals. The present  
29 study compared the establishment of mother-young relationship at birth and during the first  
30 week of life and the morphological development of the young between *Cervus elaphus*,  
31 *Cervus nippon* and their hybrids (male *nippon* X female *elaphus*). Most mother-young  
32 behaviour did not differ between the three groups, showing strong conservation of peri-partum  
33 behaviours in cervids. On the opposite, behaviour and body size of the young hybrids were  
34 similar or tended to be close to those found in the surrogate species, suggesting important  
35 maternal effects. In addition, young hybrids were more likely to be standing during the first  
36 week than young from the other groups, possibly resulting from increased maternal  
37 stimulation and/or hybrid vigour. The results from this study also indicate that smell-related  
38 and agonistic behaviours from adult females of the group towards the hybrid young were  
39 more likely to occur, suggesting potential species recognition issues that required further  
40 investigations. Our findings show that hybridization has no noticeable impact on mother-  
41 young relationship, which could partly explain the success of the hybridization between the  
42 sika and the red deer.

43 *Key-words:* *Cervus elaphus*, *Cervus nippon*, Hider species, Maternal behaviour, Mother-  
44 young recognition, Parturition, Placentophagy, Species barrier, Young behaviour.

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48 **INTRODUCTION**

49 In taxonomy, species are reproductively isolated groups of populations, but may crossbreed if  
50 one cause of isolation is removed (Futuyma, 1983). In this context, approximately 10% of  
51 species in major faunal groups that have not evolved sufficient reproductive barriers, are  
52 known to hybridize with other species (Mallet, 2007; Mallet, 2008). Hybridization may be  
53 associated with gene flow (introgression) and possibly represents an important evolutionary  
54 mechanism (Schwenk et al., 2008; Harrison and Larson, 2014). It may then contribute to  
55 genetic variation and possibly to loss of species (Allendorf et al., 2001; Laikre et al., 2010;  
56 Sakai et al., 2001) or to speciation (Mallet, 2008). Over the past centuries, humans largely  
57 contributed to this phenomenon by importing various species (e.g. in Australia: Bomford,  
58 1991; and in Europe: Apollonio et al. 2010; Di Castri et al., 2012) from their original to new  
59 habitats, thus abolishing geographical barriers between species.

60 Beyond hybridization, introgression implies different key events including interspecific  
61 mating, survival and adaptation of hybrid offspring to its environment and finally the stable  
62 integration of genetic material from one species to the other through successful repeated  
63 backcrossing (Baack and Rieseberg, 2007). In mammals, survival of the young depends  
64 strongly on the proper establishment of mother-young relationship (Clutton-Brock, 1991;  
65 Nowak et al., 2000). To ensure survival of the mother's own young, the maternal investment  
66 misdirection should be avoided, notably during lactation. Individual recognition of the young is  
67 then crucial for correct allocation of parental care (e.g. in ungulates, Lévy and Keller, 2008;  
68 Romeyer and Poindron, 1992), especially in ungulate hider species (Briefer and McElligott,  
69 2011; Torriani et al., 2006). Early parental care has an impact on growth, sexual and social  
70 behaviours in adulthood, resulting in differential reproductive success (Clutton-Brock, 1991;

71 Lindström, 1999). On one hand, given that the genotype of young hybrids results from a  
72 combination of the genomes of both parental species, an original phenotype due to  
73 hybridization may alter the recognition and then the establishment of mother-young  
74 relationship (Page et al., 2001), affecting in turn, offspring survival, growth rate or  
75 development (Peripato and Cheverud, 2002). On the other hand, hybridization may results in  
76 heterosis or hybrid vigour that increase young's survival rate. In the red deer, fawns with  
77 higher heterozygosity were most likely to survive the neonatal period (Coulson et al., 1998).  
78 Studying early relationship in hybridization context is therefore critical to better understand  
79 survival ability of hybrid progeny. Morphological development is also fundamental to  
80 characterize as it may reflect differences in parental care, in selective pressure and in future  
81 introgression aptitude of the hybrids (Senn et al., 2010). For instance in different species, size  
82 is positively correlated with survival and reproductive success (Beauplet and Guinet, 2007;  
83 Festa-Bianchet et al., 2000; Gélin et al., 2016).

84 In wild mammals, species from Cervidae are of major concern for various reasons. While  
85 more than 40 deer subspecies are threatened in the wild (IUCN 2016), some others are very  
86 common and may even be considered as a pest when overabundant (Nugent et al., 2011).  
87 Indeed, some deer species strongly impact local biodiversity through direct and cascading  
88 effects due to herbivory selectivity (Côté et al., 2004). Some of the common cervid species  
89 such as the red deer (*Cervus elaphus*) have been widely studied in the wild (e.g. Clutton-  
90 Brock et al., 1982) and in captivity (Arman, 1974) for decades, resulting in considerable  
91 knowledge of their biology. The sika deer, *Cervus nippon*, has also been well studied  
92 (McCullough et al., 2008), however, mother young relationships have been rarely investigated  
93 (Fouda et al., 1990). The sika deer is an invasive species from Asia that is spreading in  
94 Europe and has become common in the location usually inhabited by the red deer, leading to

95 conservative issues (McCullough et al., 2008). Indeed, both species are closely related  
96 polygynous species that are naturally allopatric, but do hybridize when populations become  
97 sympatric (Senn and Pemberton, 2009). In Scotland, when sika and red deer populations are  
98 found together, the proportion of red deer individuals introgressed by sika generally remains  
99 at low level (6.9%) but may reach 43% in some areas (Senn and Pemberton, 2009),  
100 suggesting that if reproductive barriers remain, they are not absolute. Interestingly, the same  
101 study failed to find any F1 hybrids, suggesting that the hybridization event is rare but not  
102 without consequences.

103         The aim of the study was to test the hypothesis of differences in establishment of  
104 mother-young relationship between red and sika deer and their hybrids. Female red deer  
105 were inseminated with sika deer semen to generate hybrid gestations, according to the  
106 preferred direction of the introgression between the two species (sika deer male x red deer  
107 female, Senn and Pemberton, 2009). We then compared the establishment of mother-young  
108 interactions at birth and during the first week of life as well as the morphological development  
109 of the young across *Cervus elaphus*, *Cervus nippon* and their hybrids.

110

## 111 **MATERIALS AND METHODS**

### 112 **Animal housing and reproduction**

113         In 2013-2015, interactions between red deer mothers giving birth to hybrid fawns  
114 (sika x red deer, “ELANIP” group,  $N = 9$ ) were monitored and compared to sika and red deer  
115 mothers giving birth to young from their own species (respectively, “NIP”,  $N = 8$  and “ELA”  
116 groups,  $N = 19$ ) at the Réserve Zoologique de la Haute-Touche (46°53'N, 1°04'E), Muséum  
117 National d'Histoire Naturelle, Indre, France. The three groups were located in different

118 enclosures (ranging from 0.8 to 1.4 ha) with a density of 10-12 females/ha. The paddocks  
119 vegetation included mostly grass, carex and thistle on which they could freely graze. A  
120 shaded area with trees was available in each paddock. Animals were fed with commercial  
121 ration (Browser Maintenance 5654, Mazuri, Witham, Essex, UK), ad libitum hay and had free  
122 access to water. Young and mother were marked individually with coloured collars. Mass of  
123 females ranged from 103 to 128 kg (mean  $\pm$  SD: 113  $\pm$  7 kg) in red deer, and 35 – 49.5 kg  
124 (mean  $\pm$  SD: 42  $\pm$  4 kg) in sika deer.

125 To control the timing of parturition, oestrus cycles were synchronized in all the female  
126 red deer by inserting intra-vaginal sponges (2 $\times$ 45 mg, Intervet Schering-Plough Animal  
127 Health, Angers, France) filled with fluorogestone acetate (Wyman et al., 2011). After 8 days,  
128 cloprostenol (75 $\mu$ g; Estrumate, Intervet Shering-Plough Animal Health, Beaucouzé, France)  
129 was injected. Sponges were removed on day 12 and females were injected with 400 UI of  
130 pregnant mare serum gonadotropin in order to induce oestrous and ovulation. Both ELA and  
131 NIP groups were then presented to their conspecific males ( $N = 2$  and  $3$  for ELA and NIP,  
132 respectively) and bred naturally. To produce hybrids, anesthetized hinds from ELANIP group  
133 were inseminated with pooled frozen/thawed semen from 3 males sika 50 hours after sponge  
134 removal using ovine insemination gun (IMV, L'Aigle, France) following similar estrus  
135 synchronization protocol to Wyman et al. (2011). Over the 17 females inseminated in 2013,  
136 10 were pregnant at ultrasonography (D45) and over the 9 females inseminated the following  
137 year, 5 were pregnant. During our study, reproductive rate was 69% in NIP ( $N = 13$ ), 97% in  
138 ELA ( $N = 34$ ) and 58% in ELANIP ( $N = 15$ ) groups. Conception dates were confirmed by  
139 weekly monitoring of plasma progesterone, estradiol and Pregnancy Associated  
140 Glycoproteins (PAGs) levels. Conception dates and gestation lengths from NIP group were  
141 determined by selecting individuals and corresponding data within a larger reproduction

142 group. Only females for which it was possible to confirm estrus (low levels of progesterone,  
143 presence of estradiol) followed by elevation of progesterone and detection of PAGs 3 weeks  
144 later were considered.

145           Some animals were excluded from the experiment. In the ELA group, one young was  
146 born dead. In the ELANIP group, while all the young received proper maternal care at birth,  
147 three of them having welts were found dead in 2014. A few females in the ELA and NIP  
148 groups left their young uncared at birth. This included 3 primiparous red deer females and 1  
149 multiparous sika deer female that had her teats injured by the enclosure. Also, two females (1  
150 in the ELANIP group and 1 in the ELA group) gave birth to twins and were excluded from our  
151 analyses. Red deer is a mono-ovulant species and twins in nature are very rare. Twinning  
152 observed in the present study may result from estrous synchronization and artificial  
153 insemination performed. In addition gestation length, milk production, birth weight, mass gain  
154 of the calf and survival rates may have been influenced by multiple births, as reported for  
155 other mono-ovulant species. Therefore, twins were excluded from the analysis. We  
156 determined sex of young at first capture, measured body mass (2014 - 2015) and mandible  
157 and leg length (2015) of newborn within the first 24 hours after birth and at weaning. Weaning  
158 was performed when mean age of the young within a group reached  $\pm 100$  days. Fawns were  
159 isolated from mothers and housed in a specific barn with access to small paddocks for a 3-  
160 month period.

161

## 162 **Behavioural observations**

163           We observed mother-young interactions in 55 dyads from late May to September.  
164 Behaviours of the young and the mother (defined in Table 1) were collected using both focal



165 and scan sampling. The first two hours after parturition were videotaped and the latency,  
166 occurrence and duration of behaviours were determined using J-Watcher 1.0 (Blumstein et  
167 al., 2006). Data available for early mother-young behaviours at parturition were based on 19  
168 ELA females, mean age 6.3 years, including 7 primiparous and 12 multiparous females; 9  
169 ELANIP females, mean age of the group 5.6 years, including 5 primiparous and 4 multiparous  
170 females; and 8 NIP, mean age of the group 4.5 years, including 4 primiparous and 4  
171 multiparous females. Then, in the first week after birth, presence/absence of behaviours were  
172 recorded every 15 minutes from 6:00 to 12:00 and from 14:00 to 22:00, leading to a total of  
173 7647 sightings. In addition, 212 focal sampling were conducted when the dyad was  
174 interacting at least once a day during the first week. The data during the first week post-  
175 partum were only collected in 2015.

176

## 177 **Statistical analyses**

178 We analyzed behaviours during the first two hours postpartum and mass gain using linear  
179 models (LM) with gaussian or poisson error distribution. As we had repeated observations of  
180 same individuals during the first week, we used Linear Mixed Models (LMM) with binomial  
181 distribution to avoid any bias due to pseudoreplication. For multiple comparisons between  
182 categories, we used Tukey's post-hoc test ('library(multcomp)'). Because the independent  
183 variables are centered and standardized, the value of the estimate indicates the importance of  
184 its effect on the response variable for simple variable and interactions (Schielezeth, 2010).  
185 Some morphometric measurements of young were not taken at birth and behaviours of some  
186 females were recorded for less than 2 hours. In this case, only the latency was used. Sample  
187 sizes for each test and for each group are specified as it varies according to the variable of  
188 interest. We controlled for factors known to affect behaviours and mass gain, such as age

189 (mother in years and young in days), body mass, sex of the young and inter-capture interval.  
190 As we only aim at controlling for the effect of intraspecific variability in mother body mass, we  
191 used centred values calculated separately for each group. Growth rates are typically size-  
192 dependent (Hector and Nakagawa, 2012), therefore young size at first capture was also  
193 accounted for. All analyses were performed with R version 2.14.1 (R Foundation for Statistical  
194 Computing, Vienna, Austria) and user interface Rstudio, version 0.97.551 (Rstudio Integrated  
195 Development Environment, Boston, MA, U.S.A.). We used backward stepwise elimination of  
196 non-significant variables, leading to the minimal adequate model (Crawley, 2007; Zuur et al.,  
197 2009).

198

### 199 **Ethical considerations**

200 According to European and French regulation on animal experimentation, experimental  
201 procedures were approved under reference 01697.02 by French Research ministry after  
202 ethical evaluation (Comité d’Ethique en Experimentation Animale N° 68, Cuvier).

203

## 204 **RESULTS**

### 205 **Gestation and morphometry at birth.**

206 NIP group had a shorter gestation length than ELA group, ELANIP group having an  
207 intermediate value (respectively,  $219 \pm 3$  days ( $N = 7$ ),  $234 \pm 4$  days ( $N = 13$ ) and  $226 \pm 4$   
208 days ( $N = 12$ );  $P < 0.001$ ) when controlling for the sex of the young. Females that had a male  
209 calf tended to have longer gestation compared to the ones that had a daughter ( $2.1 \pm 1.2$   
210 days;  $P = 0.099$ ). Time of birth ( $P = 0.24$ ) and sex ratio ( $P = 0.56$ ) did not significantly vary  
211 between ELANIP ( $N = 6$ ), ELA ( $N = 16$ ) and NIP ( $N = 10$ ) groups.

212 Morphometric measurements of young significantly differed between the three groups at birth.  
213 ELANIP group was intermediate in terms of body mass, leg and mandible lengths between  
214 ELA and NIP groups (Tables 2 and 3 and A1; Figures 1a-1f). Males were generally heavier  
215 than females at birth (Tables 2 and A1).

216

## 217 **Mother-young relationship**

### 218 Maternal behaviours

#### 219 *At parturition*

220 We found no significant difference between groups in the duration of foetal expulsion ( $22 \pm 21$   
221 minutes, mean  $\pm$  SD;  $P = 0.82$ ; Table A2; Figure 3a), in the latency ( $43 \pm 58$  seconds, mean  $\pm$   
222 SD;  $P = 0.22$ ; Table A2; Figure 3b) and duration of licking ( $57 \pm 10$  minutes, mean  $\pm$  SD;  $P =$   
223  $0.95$ ; Table A2; Figure 3d) and in the latency to express placentophagy ( $89 \pm 21$  minutes,  
224 mean  $\pm$  SD;  $P = 0.40$ ; Table A2; Figure 3c). Nonetheless, ELANIP mothers spent more time  
225 eating placenta compared to ELA group ( $P = 0.04$ ; Table A2; Figure 3e). ELANIP mothers  
226 opened their mouth more often than ELA and NIP mothers ( $P < 0.001$ ; Table A2; Figure 3f).

227 We generally found no significant difference according to the sex of the young.  
228 However, foetal expulsion tended to last longer in males than in females ( $P = 0.052$ ). Age did  
229 not affect maternal behaviours at parturition but experience did: primiparous females spent  
230 more time expelling their young ( $P = 0.020$ ). Parity also affected number of mouth opening in  
231 different ways according to the group of interest ( $P = 0.024$ ). Primiparous females had a  
232 higher number of mouth opening in ELA group while it was lower in ELANIP compared to  
233 multiparous ones. No difference was observed for mouth opening in NIP group. Other  
234 maternal behaviours were not affected by parity.

235 ELANIP fawns were more frequently sniffed ( $P < 0.001$ ; Figure 2a) and kicked ( $P <$   
236  $0.001$ ; Figure 2b) by other mothers in the group than non-hybrids during the first two hours  
237 after parturition.

238

### 239 *First week after parturition*

240 During the first post-partum week, ELANIP mothers spent more time licking their young  
241 than NIP and ELA mothers (respectively, 12% ( $N = 1512$  sightings, 4 individuals), 6% ( $N =$   
242  $3293$  sightings, 9 individuals) and 8% ( $N = 2646$  sightings, 7 individuals) of the scan; Table 4).

243 During the first post-partum week, ELANIP mothers spent more time licking their young than  
244 NIP and ELA mothers (respectively, 12% ( $N = 1512$  sightings, 4 individuals), 6% ( $N = 3293$   
245 sightings, 9 individuals) and 8% ( $N = 2646$  sightings, 7 individuals) of the scan; Table 4).  
246 Licking occurrence generally decreased with age of the young (Table 3). However, graphical  
247 examination suggests that older ELANIP and NIP fawns were licked less often while it did not  
248 change for ELA fawns. Heavier mothers were more likely to lick their young (Table 3). Sex  
249 and age of the young, as well as parity status of the mother did not affect maternal behaviours  
250 during the first week.

251

### 252 Young behaviour

#### 253 *At parturition*

254 We found no significant difference between groups in the latency to first standing  
255 attempts ( $P = 0.07$ ; Table A2; Figure 4a), in the duration of standing ( $P = 0.53$ ; Table A2;  
256 Figure 4e) and in the duration of teat searching ( $P = 0.35$ ; Table A2; Figure 4d). However,

257 ELANIP and ELA fawns stood quicker ( $P = 0.006$ ; Table A2; Figure 4b) and found the teat  
258 earlier than NIP fawns ( $P < 0.001$ ; Table A2; Figure 4c). ELANIP fawns spent more time  
259 suckling than NIP fawns, but ELA neonates did not differ from the two other groups ( $P =$   
260  $0.043$ ; Table A2; Figure 4f).

261 Sex of the young did not affect the latency to first standing attempts ( $P = 0.57$ ), the  
262 latency ( $P = 0.35$ ) and duration of standing ( $P = 0.14$ ), the duration of teat searching ( $P =$   
263  $0.33$ ), the latency ( $P = 0.77$ ) and duration of suckling ( $P = 0.84$ ).

264

#### 265 *First week after parturition*

266 Sex of the young and parity status of the mother had no effect on young behaviour.  
267 Duration of suckling was not significantly different between the three groups (respectively, 6%  
268 ( $N = 1512$  sightings, 4 individuals), 5% ( $N = 3293$  sightings, 9 individuals) and 5% ( $N = 2646$   
269 sightings, 7 individuals) of the scan; Table 4).

270 Suckling occurred more often for heavier than lighter mothers (Table 4). Suckling  
271 duration decreased with time and the effect of age on standing and licking activities varied  
272 among groups: ELANIP young were more likely to be standing than ELA and NIP fawns  
273 (respectively, 19%, 13% and 10% of the scans; Table 4). In all groups, young were closer to  
274 their mother when they were standing ( $P < 0.001$ ). Time spent standing increased significantly  
275 only in ELANIP and ELA young (Table 4).

276 Relationships between early behaviour and potentially important life-history traits such  
277 as body mass were also investigated. Young that were quicker to stand gained more mass ( $P$   
278  $= 0.009$ ), other early behaviour, however, did not affect significantly mass gain ( $P > 0.05$ ).

279

## 280 **DISCUSSION**

281 To our knowledge, this is the first study to characterize the establishment of mother-  
282 young relationships and young growth of interspecific hybrids in large wild mammals while  
283 comparing them to both parent species. Overall, more than 50% of the mother-young  
284 behaviour (8/15) investigated did not differ significantly. Behaviour and body size of the young  
285 hybrids were similar or tended to be close to the surrogate species, suggesting strong genetic  
286 impact and/or effects of the maternal environment. In addition, young hybrids were more likely  
287 to be standing during the first week than those from the other groups, possibly resulting from  
288 increased maternal stimulation and/or hybrid vigour. Our study also showed that smell-related  
289 and agonistic behaviours from adult females of the group towards the hybrid young were  
290 more likely to occur, suggesting potential species recognition issues that required further  
291 investigations. Altogether, this study demonstrates that young hybrids are totally viable and  
292 the crucial mother-young relationship does not suffer any morbid consequences.

293

### 294 **Similarity of peripartum behaviour**

295 The birth process and the following mother-young interactions were quite similar among the  
296 three groups. Females expressed crucial behaviours such as standing, licking and suckling  
297 and showed a strong attraction for amniotic fluids, fawns being cleaned immediately following  
298 birth. The expression of maternal behaviour in red deer is similar to previous observations  
299 and fawns were then readily accepted at first sucking (Arman, 1974; Arman et al., 1978;  
300 Clutton-Brock et al. 1982). However, studies documenting later interactions between the red  
301 deer mothers and the calves are lacking thus preventing further comparisons. In sika deer,  
302 Fouda et al. (1990) reported also a short latency for first standing and suckling following birth.

303 In addition, these previous studies documented a marked reduction (35%) of suckling bouts  
304 and suckling duration between birth and one week of life as observed in our study.

305 Experience of female (comparison of primiparous versus multiparous females) was assessed  
306 in the present study and few effects were observed on maternal behaviours. The strongest  
307 effect of parity was observed on labour duration, primiparous females taking longer to deliver  
308 their fawn. This effect of maternal experience on labour duration has been previously reported  
309 in various species including sheep (Dwyer & Lawrence, 2005) and can be related to a lower  
310 degree of maturation of the physiological processes of parturition in primiparous females  
311 (Nowak et al., 2000; Meurisse et al., 2005).

312 As a whole, our results are largely in accordance with previous descriptions of early maternal  
313 and young behaviours of the red and the sika deer. Interestingly, we have documented, in the  
314 context of a sika young born from a surrogate red deer mother, through in vitro fertilization  
315 and interspecific embryo transfer and gestation (see Locatelli et al., 2008), that mother-young  
316 behavior was appropriate. This result further demonstrates that there is no behavioural  
317 incompatibility between those species as suggested by their very close phylogenetic  
318 relationship (Fernández and Vrba, 2005; Polziehn and Strobeck, 1998) and similar  
319 reproductive tactics (Geist, 1998). Indeed, in precocial species, which include most ungulates,  
320 mother-young relationship is characterized by a small litter of fully developed young capable  
321 of following the mother shortly after birth. The rapid development of mother-young  
322 recognition, which allows exclusive care is a main feature of these species. In addition, some  
323 species, including sika and red deer, show a hiding strategy, *i.e.* during the first days post-  
324 partum offspring hide in the vegetation between two suckling episodes to avoid detection by  
325 predators (Lent, 1974; Nowak et al., 2000).

326

327           Altogether, these results suggest that mother-young relationship is well conserved in  
328 cervid species and ungulates in general because of strong evolutive and ecological  
329 constraints (Lent, 1974; Clutton-Brock, 1991) that trigger, both in the mother and in the young,  
330 the rapid establishment of a reciprocal bond after birth. Maternal care in mammals is  
331 associated with substantial costs, including the expenditure of energy for milk production and  
332 the increased risk of predation resulting from the presence of conspicuous neonates, the  
333 limited mobility (Clutton-Brock, 1991) and the habitat shift (Berger, 1991). Ensuring her  
334 investment in the young survival is then of prime importance (Trivers, 1972). For the young, it  
335 is a question of individual survival, as the mother is the main source of food until weaning.  
336 Mother's milk provides not only the energy intake necessary to ensure infantile survival and  
337 growth but also transmits immunity against pathogens through ingestion of colostrum and milk  
338 (Grindstaff et al., 2003). Consequently, little variability of crucial peripartum behaviours are  
339 expected among cervids.

340

#### 341 **Effect of hybridization**

342 Gestation lengths observed for both sika and red deer are in accordance with previous  
343 findings (Asher, 2007; Matsuura et al., 2004). When compared to parent species, sika x red  
344 deer hybridization was associated with a strong effect on gestation lengths and fawn birth  
345 mass. Intermediate gestation length of hybrids (226 days versus 219 days in sika and 234  
346 days in red deer) allowed birth of healthy fawns slightly smaller than red deer but far bigger  
347 than sika deer. Interestingly, phenotypic traits of the young hybrid at birth were extremely  
348 close to red deer, making difficult to distinguish between hybrids and red deer under the  
349 mother. Persisting differences of size observed at birth and at weaning are likely to remain in  
350 adult as found by previous studies (Senn et al., 2010).



351 To our knowledge, few consistent data concerning gestation length or birth weight are  
352 available for hybridization between red and sika deer. Hybridization may lead to a reduction in  
353 gestation length and fawn birth weight compared to the surrogate species if the females are  
354 inseminated by male of a smaller species. For instance, a study focusing on hybridization  
355 between hind wapiti (*Cervus elaphus manitobensis*) and sika also reported a decrease in  
356 weight of hybrid progeny at weaning when compared with wapiti characteristics (Willard et al.,  
357 1998). In addition, smaller offspring are expected to consume less milk, reducing the cost of  
358 weaning a young for the mother. Indeed, lactation is the costliest part of reproduction (Oftedal,  
359 1985) and weaning a young can affect more strongly future reproductive success than shorter  
360 reproductive effort (Gélin et al., 2015). Shorter gestation may also increase fitness progeny  
361 through earlier birthdate as young born earlier in the year generally increase their probability  
362 of survival (Clements et al., 2011). This could then decrease reproductive effort, suggesting a  
363 possible advantage for mothers to produce hybrids in some situation. At the opposite,  
364 breeding with males of a bigger species may cause complications and would then only be  
365 expected if hybrids show a substantial increase of reproductive success compared to the  
366 nonhybrids to cope with an increase in reproductive cost for the mother (Moore and Littlejohn,  
367 1989).

368 In addition, hybrids stood quicker than sika fawns at birth and spent on average more  
369 time standing the first week than the young from the two other groups. We can consider that  
370 the differences observed in standing during the first week likely reflect genetic differences as  
371 both hybrid and red deer fawns experienced identical environmental conditions. This supports  
372 previous study on hybrid vigour relating to standing behaviour in cervids (Endicott-Davies et  
373 al., 1996). In addition, young that stood quicker gained more mass, possibly increasing future  
374 survival and reproductive success (Clutton-Brock et al., 1987; Festa-Bianchet et al., 2000).

375 Contrary to what was suggested in previous studies (Senn et al., 2010), the present results  
376 does not indicate that hybrid offspring might be less viable than those from parent species.  
377 Furthermore, ungulates are precocious species where social imprinting can occur as  
378 previously demonstrated in sheep and goats (Kendrick et al., 1998, 2001). The consequence  
379 of this process being, that young form a preference for their adoptive species, and this  
380 preference may last until adulthood in the context of sexual behavior. Thus, it can be  
381 hypothesized that male and female hybrid deer will look for red deer hinds or stag  
382 respectively, as sexual partners, therefore reinforcing the process of introgression.

383         Some aspects of maternal behaviour were also affected by hybridization. Red deer  
384 mothers giving birth to hybrid fawn increased duration in placentophagy during the first two  
385 hours after parturition compared to the ones rearing neonates from their own species. A  
386 shorter duration of placentophagy would have been expected in red deer mother of hybrids,  
387 as the size of placenta is supposed to be proportional to calf birth weight. Whether this longer  
388 duration was linked to differences in placenta size or appetite factors requires further data.  
389 Red deer mothers giving birth to hybrids also showed an increased number of mouth  
390 openings at parturition. Mouth opening by mother may reflect flehmen-like behaviours  
391 favouring the transfer of odours into the vomeronasal organ (Døving and Trotier, 1998).  
392 However, unlike typical flehmen response, no curling back of the upper lip was observed.  
393 More than flehmen, sniff-yawning behaviour, reported to occur in female from Bovinae in  
394 context of parturition, was closer to the behaviour we observed in the present study (Halder &  
395 Schenkel, 1972; O'brien, 1982). The behaviour we observed, specifically developed when  
396 licking and eating the placenta, may clearly indicate an olfactory-guided activity and  
397 potentially reflects some differences in the chemosensory characteristics of the placenta  
398 (O'brien, 1982; Schaal et al., 2001). Whether differences observed in flehmen-like or sniff

399 yawning were induced by differences in chemoreceptory process driven by hybridization  
400 remains to determine. In addition, licking duration towards the young was still more important  
401 in mothers of hybrids than in the other groups during the first week after parturition, likely  
402 reflecting reaction to novelty or unfamiliarity (Krames, 1970). Young hybrids were also sniffed  
403 and attacked more often by the other mothers suggesting that species recognition could be  
404 mediated through olfaction. Altogether these data may suggest potential species recognition  
405 issues in hybridization context but further investigations are required to confirm this  
406 hypothesis. Our observations were done in a captivity context, which is likely to affect some of  
407 the results observed. One important difference is linked to the density of parturient females  
408 within a same enclosure. In the wild, red deer females isolate themselves for parturition but  
409 complete isolation for parturient females in the present study was clearly not possible. Thus, it  
410 is likely that aggressive behavior of other parturient females toward alien young in ELANIP  
411 group may directly result from the context of captivity and would not be observed in the wild.  
412 Similarly, promiscuity of the mother and the young was increased by living conditions  
413 provided to animals, possibly leading to enhancement of mother-young interactions. Finally,  
414 selection pressure removal by providing ad libitum resources may have promoted both  
415 development of the young and survival rates. Nonetheless, living conditions in the present  
416 study were identical between groups, confirming effects of hybridization observed.

417 In conclusion, this study is one of the rare providing detailed information about  
418 gestation length, early mother-young relationship and morphometric measurements in an  
419 interspecific hybrid of large mammal. It shows that hybridization has no noticeable impact on  
420 mother-young relationship, allowing survival of a potentially more vigorous young hybrid with  
421 phenotypic traits closer to those of the surrogate species. New evidences for the risk of  
422 introgression of sika genetics into the red deer are provided, allowing a better understanding

423 of the success of interspecific hybridization in the wild and bringing possible insights for  
424 management of hybrid populations.

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437

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441

### 442 **AUTHOR'S CONTRIBUTIONS**

443 U.G. conceived behavioural protocol, performed field study, analyzed the data and wrote the  
444 manuscript. M.K., F.L. and R.N. conceived the project, secured the fundings and wrote the  
445 manuscript. V.dB contributed to fieldwork and to video analysis. Y.L. conceived the project,  
446 secured the fundings, performed experiment and wrote the manuscript.

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## 450 REFERENCES

- Allendorf, F. W., Leary, R. F., Spruell, P., & Wenburg, J. K. (2001). The problems with hybrids: setting conservation guidelines. *Trends in Ecology & Evolution*, *16*(11), 613–622.
- Apollonio, M., Andersen, R., & Putman, R. (2010). *European ungulates and their management in the 21st century*. Cambridge University Press.
- Arman, P. (1974). A note on parturition and maternal behaviour in captive red deer (*Cervus elaphus* L.). *Journal of Reproduction and Fertility*, *37*(1), 87–90.
- Arman, P., Hamilton, W., & Sharman, G. (1978). Observations on the calving of free-ranging tame red deer (*Cervus elaphus*). *Journal of Reproduction and Fertility*, *54*(2), 279–283.
- Asher, G. (2007). Gestation length in red deer: genetically determined or environmentally controlled? *Society of Reproduction and Fertility Supplement*, *64*, 255–260.
- Baack, E. J., & Rieseberg, L. H. (2007). A genomic view of introgression and hybrid speciation. *Current Opinion in Genetics & Development*, *17*(6), 513–518.
- Beauplet, G., & Guinet, C. (2007). Phenotypic determinants of individual fitness in female fur seals: larger is better. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *274*, 1877–1883.
- Berger, J. (1991). Pregnancy incentives, predation constraints and habitat shifts: experimental and field evidence for wild bighorn sheep. *Animal Behaviour*, *41*, 61–77.
- Blumstein, D. T., Daniel, J. C., & Evans, C. S. (2006). *JWatcher 1.0*. Retrieved from <http://www.jwatcher.ucla.edu>
- Bomford, M. (1991). *Importing and keeping exotic vertebrates in Australia: criteria for the assessment of risk*. Australian Government Pub. Service.
- Briefer, E., & McElligott, A. G. (2011). Mutual mother–offspring vocal recognition in an ungulate hider species (*Capra hircus*). *Animal Cognition*, *14*(4), 585–598.
- Clements, M. N., Clutton-Brock, T. H., Albon, S. D., Pemberton, J. M., & Kruuk, L. E. (2011). Gestation length variation in a wild ungulate. *Functional Ecology*, *25*(3), 691–703.

- Clutton-Brock, T.H., Guinness, F.E., & Albon, S.D. (1982). *Red deer: behavior and ecology of two sexes* (The University of Chicago Press, Ed.). Chicago.
- Clutton-Brock, T. H. (1991). *The evolution of parental care*. Princeton University Press, Princeton.
- Clutton-Brock, T. H., Major, M., Albon, S. D., & Guinness, F. E. (1987). Early development and population dynamics in red deer. I. Density-dependent effects on juvenile survival. *Journal of Animal Ecology*, *56*, 53–64.
- Côté, S. D., Rooney, T. P., Tremblay, J.-P., Dussault, C., & Waller, D. M. (2004). Ecological impacts of deer overabundance. *Annual Review of Ecology and Systematics*, *35*, 113–147.
- Coulson, T. N., Pemberton, J. M., Albon, S. D., Beaumont, M., Marshall, T. C., Slate, J., ... Clutton-Brock, T. H. (1998). Microsatellites reveal heterosis in red deer. *Proceedings of the Royal Society of London B: Biological Sciences*, *265*, 489–495.
- Crawley, M. J. (2007). *The R Book*. John Wiley & Sons, Chichester.
- Di Castri, F., Hansen, A. J., & Debussche, M. (2012). *Biological invasions in Europe and the Mediterranean Basin* (Vol. 65). Springer Science & Business Media.
- Døving, K. B., & Trotier, D. (1998). Structure and function of the vomeronasal organ. *Journal of Experimental Biology*, *201*(21), 2913–2925.
- Dwyer, C. M., & Lawrence, A. B. (2005). A review of the behavioural and physiological adaptations of hill and lowland breeds of sheep that favour lamb survival. *Applied Animal Behaviour Science*, *92*(3), 235–260.
- Endicott-Davies, D., Barrie, A., & Fisher, M. (1996). Differences in the hiding behaviour of new-born red deer and hybrid 1/4 Père David's × 3/4 red deer calves. *Animal Science*, *62*(2), 363–367.
- Fernández, M. H., & Vrba, E. S. (2005). A complete estimate of the phylogenetic relationships in Ruminantia: a dated species-level supertree of the extant ruminants. *Biological Reviews*, *80*(2), 269–302.

- Festa-Bianchet, M., Jorgenson, J. T., & Réale, D. (2000). Early development, adult mass, and reproductive success in bighorn sheep. *Behavioral Ecology*, *11*(6), 633–639.
- Fouda, M., Nicol, C., Webster, A., & Metwally, M. (1990). Maternal-infant relationships in captive Sika deer (*Cervus nippon*). *Small Ruminant Research*, *3*(3), 199–209.
- Futuyma, D. J. (1983). *Science on trial: the case for evolution*. Pantheon Books.
- Geist, V. (1998). *Deer of the world: their evolution, behaviour, and ecology*. Stackpole books.
- Gélin, U., Wilson, M. E., Coulson, G., & Festa-Bianchet, M. (2015). Experimental manipulation of female reproduction demonstrates its fitness costs in kangaroos. *Journal of Animal Ecology*, *84*(1), 239–248.
- Gélin, U., Wilson, M. E., Cripps, J., Coulson, G., & Festa-Bianchet, M. (2016). Individual heterogeneity and offspring sex affect the growth–reproduction trade-off in a mammal with indeterminate growth. *Oecologia*, *180*(4), 1127–1135.
- Grindstaff, J. L., Brodie, E. D., & Ketterson, E. D. (2003). Immune function across generations: integrating mechanism and evolutionary process in maternal antibody transmission. *Proceedings of the Royal Society of London B: Biological Sciences*, *270*(1531), 2309–2319.
- Halder, U., & Schenkel, R. (1972). Das Riech-Gähnen bei Rindern (Bovinae). *Zeitschrift Für Säugetierkunde*, *37*, 232–245.
- Harrison, R. G., & Larson, E. L. (2014). Hybridization, Introgression, and the Nature of Species Boundaries. *Journal of Heredity*, *105*(S1), 795–809.
- Hector, K. L., & Nakagawa, S. (2012). Quantitative analysis of compensatory and catch-up growth in diverse taxa. *Journal of Animal Ecology*, *81*(3), 583–593.
- Kendrick, K. M., Haupt, M. A., Hinton, M. R., Broad, K. D., & Skinner, J. D. (2001). Sex differences in the influence of mothers on the sociosexual preferences of their offspring. *Hormones and Behavior*, *40*(2), 322–338.
- Kendrick, K. M., Hinton, M. R., Atkins, K., Haupt, M. A., & Skinner, J. D. (1998). Mothers determine sexual preferences. *Nature*, *395*(6699), 229.

- Krames, L. (1970). Responses of female rats to the individual body odors of male rats. *Psychonomic Science*, 20(5), 274–275.
- Laikre, L., Schwartz, M. K., Waples, R. S., & Ryman, N. (2010). Compromising genetic diversity in the wild: unmonitored large-scale release of plants and animals. *Trends in Ecology & Evolution*, 25(9), 520–529.
- Lévy, F., & Keller, M. (2008). Neurobiology of maternal behavior in sheep. *Advances in the Study of Behavior*, 38, 399–437.
- Lindström, J. (1999). Early development and fitness in birds and mammals. *Trends in Ecology & Evolution*, 14(9), 343–348.
- Locatelli, Y., Vallet, J.-C., Baril, G., Touzé, J.-L., Hendricks, A., Legendre, X., ... Mermillod, P. (2008). Successful interspecific pregnancy after transfer of in vitro-produced sika deer (*Cervus nippon nippon*) embryo in red deer (*Cervus elaphus hippelaphus*) surrogate hind. *Reproduction, Fertility and Development*, 20(1), 160–161.
- Mallet, J. (2007). Hybrid speciation. *Nature*, 446(7133), 279.
- Mallet, J. (2008). Hybridization, ecological races and the nature of species: empirical evidence for the ease of speciation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363(1506), 2971.
- Matsuura, Y., Sato, K., Suzuki, M., & Ohtaishi, N. (2004). The effects of age, body weight and reproductive status on conception dates and gestation periods in captive sika deer. *Mammal Study*, 29(1), 15–20.
- McCullough, D. R., Takatsuki, S., & Kaji, K. (2008). *Sika deer: biology and management of native and introduced populations*. Springer Science & Business Media.
- Meurisse, M., Gonzalez, A., Delsol, G., Caba, M., Lévy, F., & Poindron, P. (2005). Estradiol receptor- $\alpha$  expression in hypothalamic and limbic regions of ewes is influenced by physiological state and maternal experience. *Society for Behavioral Neuroendocrinology Annual Meeting Issue 2005*, 48(1), 34–43.



- Moore, G. H., & Littlejohn, R. P. (1989). Hybridisation of farmed wapiti (*Cervus elaphus manitobensis*) and red deer (*Cervus elaphus*). *New Zealand Journal of Zoology*, *16*, 191–198.
- Nowak, R., Porter, R. H., Lévy, F., Orgeur, P., & Schaal, B. (2000). Role of mother-young interactions in the survival of offspring in domestic mammals. *Reviews of Reproduction*, *5*(3), 153–163.
- Nugent, G., McShea, W., Parkes, J., Woodley, S., Waithaka, J., Moro, J., ... Flueck, W. (2011). Policies and management of overabundant deer (native or exotic) in protected areas. *Animal Production Science*, *51*(4), 384–389.
- O'brien, P. H. (1982). Flehmen: Its occurrence and possible functions in feral goats. *Animal Behaviour*, *30*(4), 1015–1019.
- Oftedal, O. T. (1985). Pregnancy and lactation. In Hudson R J & White R G (Series Ed.), *Bioenergetics of wild herbivores* (pp. 215–236). CRC Press, Boca Raton.
- Page, B., Goldsworthy, S. D., & Hindell, M. A. (2001). Vocal traits of hybrid fur seals: intermediate to their parental species. *Animal Behaviour*, *61*(5), 959–967.
- Peripato, A. C., & Cheverud, J. M. (2002). Genetic Influences on Maternal Care. *The American Naturalist*, *160*(S6), S173–S185.
- Polzieln, R., & Strobeck, C. (1998). Phylogeny of wapiti, red deer, sika deer, and other North American cervids as determined from mitochondrial DNA. *Molecular Phylogenetics and Evolution*, *10*(2), 249–258.
- Romeyer, A., & Poindron, P. (1992). Early maternal discrimination of alien kids by post-parturient goats. *Behavioural Processes*, *26*(2–3), 103–111.
- Sakai, A. K., Allendorf, F. W., Holt, J. S., Lodge, D. M., Molofsky, J., With, K. A., ... Ellstrand, N. C. (2001). The population biology of invasive species. *Annual Review of Ecology and Systematics*, 305–332.
- Schaal, B., Coureaud, G., Marlier, L., & Soussignan, R. (2001). Fetal olfactory cognition preadapts neonatal behavior in mammals. In *Chemical Signals in Vertebrates 9*

- (Marchlewska-Koj A., Lepri J.J., Müller-Schwarze D. (eds), pp. 197–204). Springer, Boston, MA.
- Schielezeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, 1(2), 103–113.
- Schwenk, K., Brede, N., & Streit, B. (2008). Introduction. Extent, processes and evolutionary impact of interspecific hybridization in animals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363(1505), 2805–2811.
- Senn, H. V., & Pemberton, J. M. (2009). Variable extent of hybridization between invasive sika (*Cervus nippon*) and native red deer (*C. elaphus*) in a small geographical area. *Molecular Ecology*, 18(5), 862–876.
- Senn, H. V., Swanson, G. M., Goodman, S. J., Barton, N. H., & Pemberton, J. M. (2010). Phenotypic correlates of hybridisation between red and sika deer (genus *Cervus*). *Journal of Animal Ecology*, 79(2), 414–425.
- Torriani, M. V. G., Vannoni, E., McElligott, A. G., Associate Editor: Tim Coulson, & Editor: Jonathan B. Losos. (2006). Mother–Young Recognition in an Ungulate Hider Species: A Unidirectional Process. *The American Naturalist*, 168(3), 412–420.
- Trivers, R. (1972). Parental investment and sexual selection. In C. BG (Series Ed.), *Sexual selection and the descent of man* (pp. 136–179). Aldine publishing company, Chicago.
- Willard, S. T., Flores-Foxworth, G., Chapman, S., Drew, M. L., Hughes, D. M., Neuendorff, D. A., & Randel, R. D. (1998). Hybridization between wapiti (*Cervus elephus manitobensis*) and sika deer (*Cervus nippon*): a comparison of two artificial insemination techniques. *Journal of Zoo and Wildlife Medicine*, 295–299.
- Wyman, M. T., Charlton, B. D., Locatelli, Y., & Reby, D. (2011). Variability of female responses to conspecific vs. heterospecific male mating calls in polygynous deer: an open door to hybridization? *PLoS One*, 6(8), e23296.
- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. (2009). *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York.

451 **Table 1.** Behavioural variables recorded during our observations.

	<b>Focal sampling 2 hours after birth</b>	<b>Scan sampling First week</b>	<b>Focal sampling First week</b>
<b>Young</b>	latency to first standing attempt latency to first suckling latency to first standing (> 10 seconds) total duration of teat searching (exploring inguinal area) total duration of suckling total duration of standing	suckling standing distance to the mother (superior or inferior to 2 meters)	duration of mother-young interaction duration of suckling
<b>Mother</b>	duration of foetal expulsion latency to first licking total duration of licking number of mouth opening events latency to express placentophagy total duration of placentophagy	licking	duration of licking
<b>Others females</b>	number of sniffing events number of kicking events		

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462 **Table 2.** Effects of the group on body mass, leg and inferior mandible length at birth and at  
 463 weaning.

Measurements	N	Fixed effects		
		Group compared to <i>ELANIP</i>	Sex of the young compared to female	Mother mass (kg)
<b>Birth mass (kg)</b>	65,	ELA: 0.9 (0.3)	Male: 0.7 (0.2)	<i>0.05 (0.03)</i>
	54 individuals (32 when including mother mass)	NIP: -5.7 (0.3)		
<b>Leg length at birth (cm)</b>	24	ELA: 1.8 (0.6)	NA	0.09 (0.03)
<b>Mandible length at birth (cm)</b>	24	NIP: -6.7 (0.5)		
		ELA: 1.8 (0.4)	NA	<i>0.03 (0.02)</i>
		NIP: -3.1 (0.3)		

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465 ELANIP: hybrid sika deer X red deer, ELA: red deer, NIP: sika deer. Italic indicates non-  
 466 significant variables not included in the final model. Estimates (SD) are based on Linear  
 467 Models.

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479 **Table 3.** Effects of the group on body mass, leg and inferior mandible length at birth and at  
 480 weaning.

Measurements		Fixed effects			
	<i>N</i>	Group compared to <i>ELANIP</i>	Mother mass (kg)	Birth measurements (kg/cm)	Age at weaning (days)
<b>Mass at weaning (kg)</b>	29	ELA: 13.9 (1.7)	0.38 (0.11)	2.27 (0.60)	0.23 (0.05)
		NIP: -19.5 (1.7)			
<b>Leg length at weaning (cm)</b>	29	ELA: 2.3 (0.4)	0.14 (0.02)	0.56 (0.18)	0.06 (0.01)
		NIP: -7.6 (0.4)			
<b>Mandible length at weaning (cm)</b>	29	ELA: 1.5 (0.6)	<i>0.06 (0.04)</i>	0.84 (0.36)	0.04 (0.01)
		NIP: -3.9 (0.6)			

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482 ELANIP: hybrid sika deer X red deer, ELA: red deer, NIP: sika deer. Italic indicates non-  
 483 significant variables not included in the final model. Estimates (SD) are based on Linear  
 484 Models.

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493 **Table 4.** Occurrence of maternal licking, and suckling-standing activities in the young during  
 494 the first week after birth in each group.

Behaviour	Fixed effects					
	Group compared to <i>ELANIP</i>	Age of the young (days)	Mother mass (kg)	Age of the mother (year)	Group X Age of the young	Group X Age of the mother
<b>Licking</b>	ELA: -0.34 (0.17) NIP: -0.64 (0.16)	-0.16 (0.04)	0.03 (0.01)	NA	NA	NA
<b>Suckling</b>	ELA:0.04 (0.16) NIP:0.11 (0.16)	-0.22 (0.05)	0.04 (0.01)	<i>0.03</i> <i>(0.16)</i>	NA	ELA:0.02 (0.17) NIP:-0.48 (0.18)
<b>Standing</b>	ELA:-0.49 (0.16) NIP:-0.79 (0.16)	0.16 (0.07)	NA	NA	ELA:0.14 (0.09) NIP:-0.20 (0.09)	NA

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496 ELANIP: hybrid sika deer X red deer, ELA: red deer, NIP: sika deer, for 7451 sighting on 20

497 individuals. Italic indicates non-significant variables not included in the final model. Estimates

498 (SE) are based on Linear Mixed Models (distribution binomial).

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507 **Supplementary material**

**Table A1.** Morphometrical characteristics of female red deer and sika deer that gave birth to young of their own species (respectively, ELA and NIP), and of female red deer that gave birth to young hybrids resulting from insemination by sika deer semen (ELANIP).

Variables	Years	Groups		
		ELA	ELANIP	NIP
<b>Body mass at birth (kg)</b>	2014	9.5 ± 1.0 (range: 7.6 – 11.5); 11 females: 9.1 ± 1.2 (range: 7.6 – 11.5); 8 males: 10.0 ± 0.5 (range: 9.0 – 10.5)	8.4 ± 0.7 (range: 7.4 – 9.2); 5 females: 8.1 ± 0.6 (range: 7.4 – 8.7); 3 males: 9.0 ± 0.3 (range: 8.6 – 9.2)	2.7 ± 0.4 kg (range: 2.2 – 3.2); 3 females: 2.7 ± 0.2 (range: 2.6 – 3.0); 3 males: 2.7 ± 0.5 (range: 2.2 – 3.2)
	2015	9.9 ± 1.2 (range: 7.8 – 11.5); 6 females: 9.5 ± 1.2 (range: 7.8 – 11.3); 7 males: 10.2 ± 1.1 (range: 8.0 – 11.5)	9.1 ± 1.4 (range: 8.0 – 11.1); 3 females: 8.5 ± 0.6 (range: 8.0 – 9.2); 1 male: 11.1	3.2 ± 0.5 (range: 2.5 – 4.3); 7 females: 3.1 ± 0.4 (range: 2.5 – 3.6); 8 males: 3.3 ± 0.6 (range: 2.5 – 4.3)
	2014- 2015	9.7 ± 1.1 (range: 7.6 – 11.5); 17 females: 9.3 ± 1.2 (range: 7.6 – 11.5); 15 males: 10.1 ± 0.8 (range: 8.0 – 11.5)	8.7 ± 1.0 (range: 7.4 – 11.1); 8 females: 8.2 ± 0.6 (range: 7.4 – 9.2); 4 males: 9.5 ± 1.1 (range: 8.6 – 11.1)	3.0 ± 0.5 (range: 2.2 – 4.3); 10 females: 3.0 ± 0.4 (range: 2.5 – 3.6); 11 males: 3.1 ± 0.6 (range: 2.2 – 4.3)
<b>Leg length at birth (cm)</b>	2015	26.9 ± 0.9 (range: 25.7 – 28.3); 2 females: 26.0 ± 0.4 (range: 25.7 – 26.3); 4 males: 27.4 ± 0.7 (range: 26.3 – 28.3)	25.9 ± 1.2 (range: 25.0 – 27.3); 2 females: 25.2 ± 0.3 (range: 25 – 25.4); 1 male: 27.3	18.6 ± 0.7 (range: 17.6 – 20.0); 7 females: 18.6 ± 0.7 (range: 17.6 – 19.5); 8 males: 18.6 ± 0.7 (range: 17.9 – 20.0)
		15 ± 0.6 (range: 14.5 – 16.0); 2 females: 14.6 ± 0.1 (range: 14.5 – 14.7); 4 males: 15.2 ± 0.6 (range: 14.7 – 16.0)	13.2 ± 0.8 (range: 12.3 – 13.8); 2 females: 12.9 ± 0.8 (range: 12.3 – 13.5); 1 male: 13.8	10.1 ± 0.5 (range: 9.2 – 10.8); 7 females: 10.0 ± 0.6 (range: 9.2 – 10.8); 8 males: 10.1 ± 0.4 (range: 9.5 – 10.8)
<b>Age at weaning (days)</b>	2015	99 ± 8 (range: 79 – 106; N = 13)	103 ± 5 (range: 95 – 106; N = 4)	105 ± 17 (range: 72 – 130; N = 13)

<b>Body mass at 2015 weaning (kg)</b>	48.9 ± 7.2 (range: 31.5 – 58.0); 6 females: 45.7 ± 7.7 (range: 31.5 – 51.5); 7 males: 51.6 ± 5.8 (range: 43.5 – 58.0)	38.6 ± 1.5 (range: 37.0 – 40.5); 3 females: 38.5 ± 1.8 (range: 37.0 – 40.5); 1 male: 39.0	17.9 ± 3.3 (range: 13.5 – 23.0); 5 females: 16.1 ± 2.1 (range: 13.5 – 18.5); 7 males: 19.1 ± 3.5 (range: 14.5 – 23.0)
<b>Leg length at 2015 weaning (cm)</b>	33.7 ± 1.6 (range: 30.7 – 36.2); 6 females: 32.8 ± 1.3 (range: 30.7 – 34.5); 7 males: 34.5 ± 1.5 (range: 32.3 – 36.2)	31.9 ± 0.8 (range: 30.7 – 32.5); 3 females: 31.8 ± 1.0 (range: 30.7 – 32.5); 1 male: 32.1	24.2 ± 1.2 (range: 22.0 – 25.8); 5 females: 23.8 ± 1.1 (range: 22.0 – 24.8); 7 males: 24.4 ± 1.3 (range: 22.5 – 25.8)
<b>Jaw length at 2015 weaning (cm)</b>	20.6 ± 1.6 (range: 16.9 ± 22.6); 6 females: 20.6 ± 1.5 (range: 18.6 – 22.6); 7 males: 20.6 ± 1.9 (range: 16.9 – 22.6)	18.8 ± 0.5 (range: 18.4 – 19.5); 3 females: 18.9 ± 0.6 (range: 18.4 – 19.5); 1 male: 18.4	14.8 ± 0.7 (range: 14.0 – 16.0); 5 females: 14.6 ± 0.5 (range: 14.0 – 15.0); 7 males: 15.0 ± 0.7 (range: 14.0 – 16.0)

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508 Mean ± SD.



**Table A2.** Gestation, parturition and young survival characteristics at birth, of female red deer and sika deer that gave birth to young of their own species (respectively, ELA and NIP), and of female red deer that gave birth to young hybrids resulting from insemination by sika deer semen (ELANIP).

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<b>Behaviours</b>	<b>ELA</b>	<b>ELANIP</b>	<b>NIP</b>
Duration of expulsion (min)	25 ± 25 (N=10)	22 ± 22 (N=6)	16 ± 16 (N=8)
Latency to licking (s)	62 ± 70 (N = 18)	29 ± 23 (N = 8)	5 ± 3 (N = 6)
Latency to first standing attempts (min)	3 ± 2 (N = 16)	2 ± 1 (N = 7)	3 ± 1 (N = 8)
Latency to standing (min)	13 ± 5 (N = 19)	9 ± 4 (N = 9)	19 ± 9 (N = 8)
Latency to suckling (min)	32 ± 15 (N = 18)	19 ± 7 (N = 8)	60 ± 31 (N = 8)
Latency to placentophagy (min)	84 ± 19 (N = 18)	97 ± 25 (N = 12)	88 ± 17 (N = 5)
Duration of licking (min)	57 ± 10 (N = 11)	58 ± 12 (N = 8)	56 ± 8 (N = 6)
Duration of teat searching by young (min)	16 ± 8 (N = 12)	12 ± 6 (N = 8)	9 ± 13 (N = 6)
Duration of standing (min)	54 ± 16 (N = 12)	61 ± 19 (N = 8)	52 ± 12 (N = 6)
Duration of suckling (min)	12 ± 8 (N = 12)	15 ± 10 (N = 7)	4 ± 3 (N = 6)
Number of mouth openings	14 ± 14 (N = 12)	21 ± 19 (N = 8)	2 ± 2 (N = 6)
Duration of	11 ± 9	16 ± 13	10 ± 4

placentophagy (min)	( <i>N</i> = 12)	( <i>N</i> = 8)	( <i>N</i> = 4)
Proportion of time spent licking (%)	8 ( <i>N</i> = 2646, 7 individuals)	12 ( <i>N</i> = 1512, 4 individuals)	6 ( <i>N</i> = 3293, 9 individuals)
Proportion of time spent suckling (%)	5 ( <i>N</i> = 2646, 7 individuals)	6 ( <i>N</i> = 1512, 4 individuals)	5 ( <i>N</i> = 3293, 9 individuals)
Proportion of time spent standing (%)	13 ( <i>N</i> = 2646, 7 individuals)	19 ( <i>N</i> = 1512, 4 individuals)	10 ( <i>N</i> = 3293, 9 individuals)

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510 Mean  $\pm$  SD.

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**Table A3.** Gestation, parturition and young survival characteristics during the first week

following birth, of female red deer and sika deer that gave birth to young of their own species (respectively, ELA and NIP), and of female red deer that gave birth to young hybrids resulting from insemination by sika deer semen (ELANIP).

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<b>Variables during the first week</b>	<b>All groups</b>	<b>ELA</b>	<b>ELANIP</b>	<b>NIP</b>
Number of daily mother-young interaction	2.5 ± 1.3 (0 - 7) N = 139 (20 individuals)	2.6 ± 1.1 (0 - 5) N = 49 (7 individuals)	3.7 ± 1.4 (2 - 7) N = 28 (4 individuals)	1.8 ± 1.3 (0 - 4) N = 62 (9 individuals)
Average duration of mother-young interaction (min)	24:12 ± 19:48 (0:23 - 99:51) N = 217 (20 individuals)	29:12 ± 16:59 (1:21 - 92:21) N = 71 (7 individuals)	21:32 ± 19:18 (1:18 - 99:51) N = 53 (4 individuals)	24:10 ± 20:20 (0:23 - 94:23) N = 93 (9 individuals)
Proportion of time spent licking during observations	0.33 ± 0:19 (0.00 - 1.00) N = 217 (20 individuals)	0.36 ± 0:19 (0.06 - 1.00) N = 71 (7 individuals)	0.39 ± 0:20 (0.06 - 0.85) N = 53 (4 individuals)	0.27 ± 0:14 (0.00 - 0.89) N = 93 (9 individuals)
Proportion of time spent suckling during observations	0.30 ± 0:25 (0.00 - 1.00) N = 217 (20 individuals)	0.23 ± 0:16 (0.00 - 0.65) N = 71 (7 individuals)	0.22 ± 0:17 (0.01 - 0.82) N = 53 (4 individuals)	0.39 ± 0:21 (0.02 - 1.00) N = 93 (9 individuals)
Estimated daily duration of interaction between 6:00-11:00 and 14:00-22:00 (min)	60 ± 30	75 ± 55	79 ± 40	43 ± 30
Estimated daily duration of time spent licking between 6:00-11:00 and 14:00-22:00 (min)	20 ± 18	27 ± 20	31 ± 04	11 ± 45
Estimated daily duration of time spent licking between 6:00-11:00 and 14:00-22:00 (min)	18 ± 27	17 ± 28	17 ± 32	16 ± 58

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514 Mean  $\pm$  SD.

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542 **Figure 1.** Box-and-whisker diagrams for birth mass (a), leg (b) and mandible (c) lengths at  
543 birth and at weaning (respectively (d), (e), (f); age at weaning:  $102 \pm 12$  days) according to  
544 group; ELANIP: hybrid sika deer X red deer, ELA: red deer, NIP: sika deer. Different letters  
545 indicate significant differences at  $P < 0.05$ . The bold line represents the median of the data  
546 and the end of the box shows the upper and lower quartiles. Extreme lines of the whiskers  
547 shows the highest and lowest value excluding outliers (open circle).

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549 **Figure 2.** Box-and-whisker diagrams for number of sniffing (a) and kicking events (b) directed  
550 towards the young during the first two hours after birth by other females than its mother in  
551 each group; ELANIP: hybrid sika deer and X red deer, ELA: red deer, NIP: sika deer. Different  
552 letters indicate significant differences at  $P < 0.05$ . The bold line represents the median of the  
553 data and the end of the box shows the upper and lower quartiles. Extreme lines of the  
554 whiskers shows the highest and lowest value excluding outliers (open circle).

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557 **Figure 3.** Box-and-whisker diagrams for duration of foetal expulsion (a), latency to lick (b) and  
558 to express placentophagy (c), duration of licking (d) and of placentophagy (e, and number of  
559 mouth openings (f) in mother of each group; ELANIP: hybrid sika deer X red deer, ELA: red  
560 deer, NIP: sika deer. Different letters indicate significant differences at  $P < 0.05$ . The bold line  
561 represents the median of the data and the end of the box shows the upper and lower  
562 quartiles. Extreme lines of the whiskers shows the highest and lowest value excluding outliers  
563 (open circle).

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566 **Figure 4.** Box-and-whisker diagrams for latency to first standing attempts (a), to standing (b)  
567 and to suckling (c), duration of teat searching (d), standing (e) and suckling (f) within 2 hours  
568 after birth according to group; ELANIP: hybrid sika deer X red deer, ELA: red deer, NIP: sika  
569 deer. The bold line represents the median of the data and the end of the box shows the upper  
570 and lower quartiles. Extreme lines of the whiskers shows the highest and lowest value  
571 excluding outliers.

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Figure 1

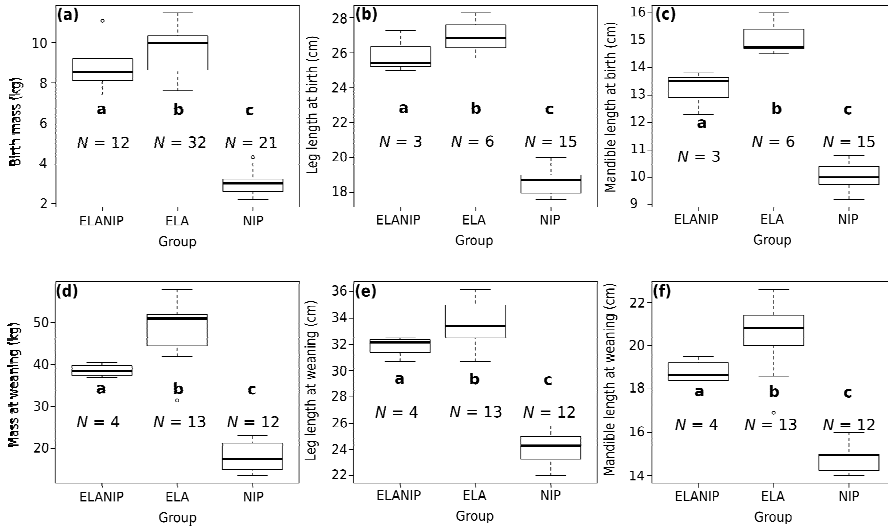


Figure 2

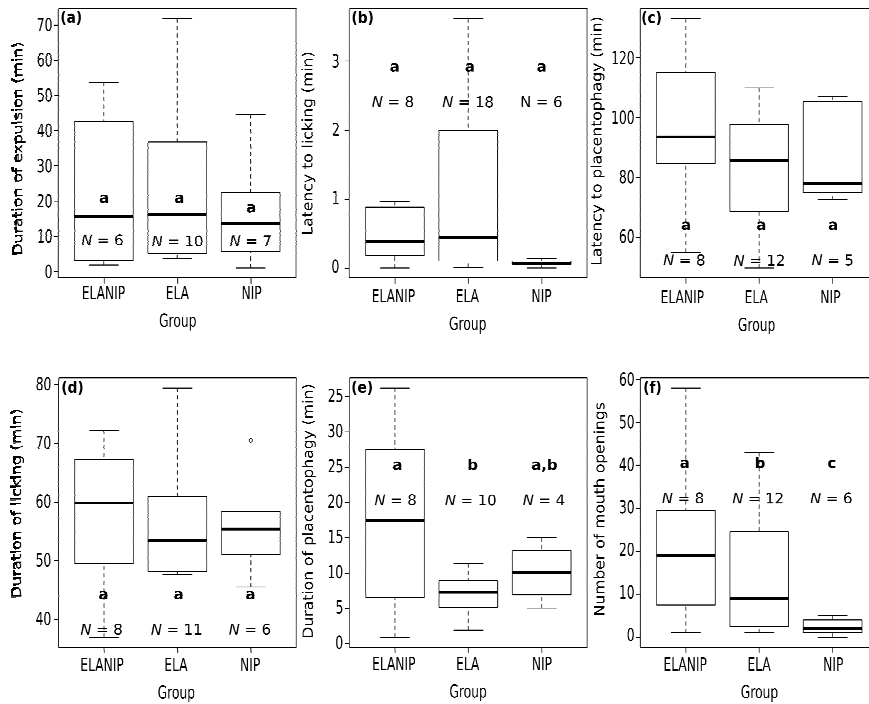


Figure 3

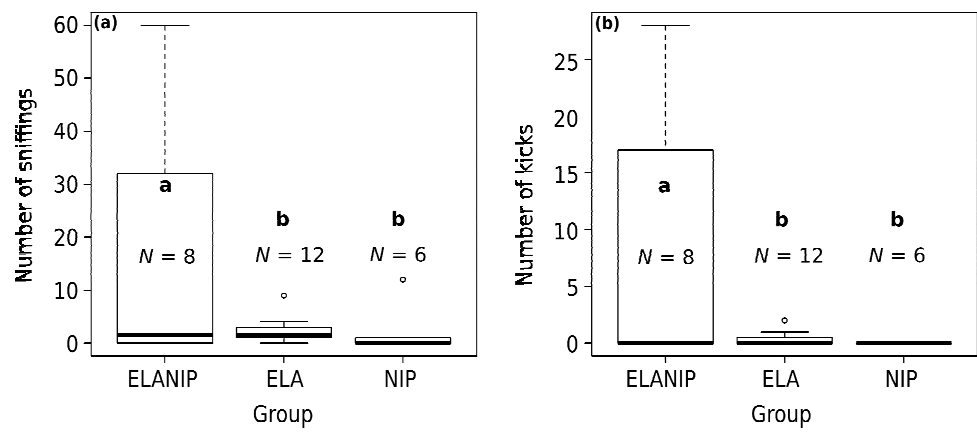


Figure 4

