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Impact of hybridization between sika and red deer on phenotypic traits of the newborn and mother–young relationships

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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.

45

46

47

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 μ 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 ± 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 ± 3 days ($N = 7$), 234 ± 4 days ($N = 13$) and 226 ± 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 ± 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 ± 21
221 minutes, mean \pm SD; $P = 0.82$; Table A2; Figure 3a), in the latency (43 ± 58 seconds, mean \pm
222 SD; $P = 0.22$; Table A2; Figure 3b) and duration of licking (57 ± 10 minutes, mean \pm SD; $P =$
223 0.95 ; Table A2; Figure 3d) and in the latency to express placentophagy (89 ± 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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451 **Table 1.** Behavioural variables recorded during our observations.

	Focal sampling 2 hours after birth	Scan sampling First week	Focal sampling First week
Young	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
Mother	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
Others females	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)
Birth mass (kg)	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)		
Leg length at birth (cm)	24	ELA: 1.8 (0.6)	NA	0.09 (0.03)
Mandible length at birth (cm)	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)
Mass at weaning (kg)	29	ELA: 13.9 (1.7) NIP: -19.5 (1.7)	0.38 (0.11)	2.27 (0.60)	0.23 (0.05)
Leg length at weaning (cm)	29	ELA: 2.3 (0.4) NIP: -7.6 (0.4)	0.14 (0.02)	0.56 (0.18)	0.06 (0.01)
Mandible length at weaning (cm)	29	ELA: 1.5 (0.6) NIP: -3.9 (0.6)	<i>0.06 (0.04)</i>	0.84 (0.36)	0.04 (0.01)

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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
Licking	ELA: -0.34 (0.17) NIP: -0.64 (0.16)	-0.16 (0.04)	0.03 (0.01)	NA	NA	NA
Suckling	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)
Standing	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
Body mass at birth (kg)	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)
Leg length at birth (cm)	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)
	2015	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)
Age at weaning (days)	2015	99 ± 8 (range: 79 – 106; N = 13)	103 ± 5 (range: 95 – 106; N = 4)	105 ± 17 (range: 72 – 130; N = 13)

Body mass at 2015 weaning (kg)	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)
Leg length at 2015 weaning (cm)	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)
Jaw length at 2015 weaning (cm)	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)

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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Behaviours	ELA	ELANIP	NIP
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)

510 Mean ± 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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Variables during the first week	All groups	ELA	ELANIP	NIP
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 ± 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).

548

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

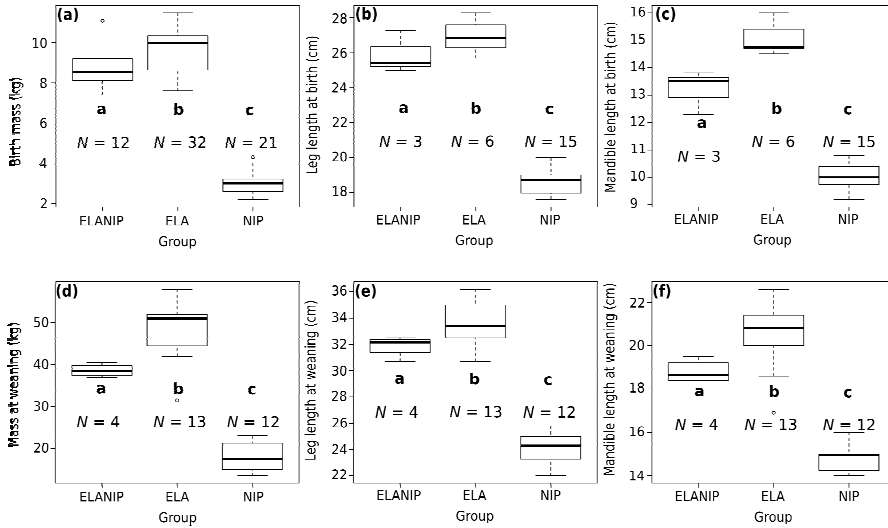


Figure 2

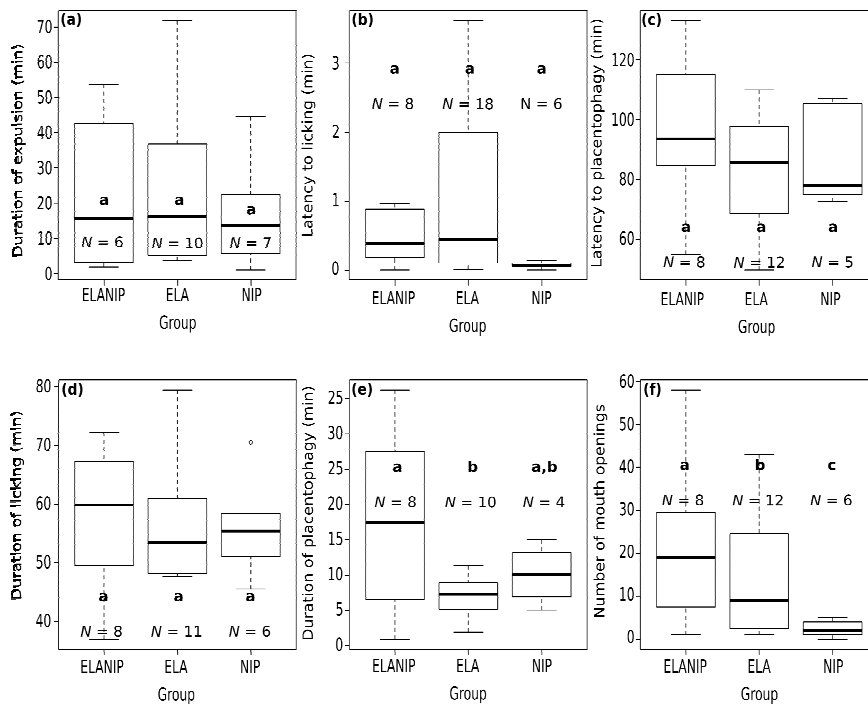


Figure 3

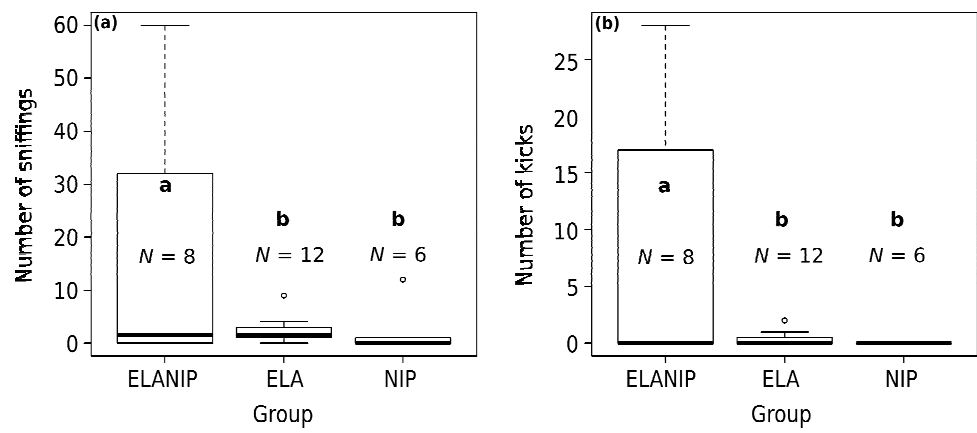


Figure 4

