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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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The removal of pre-existing geographical barriers between species, notably by humans, allows previously isolated species to hybridize. Interspecies hybridization has been studied at different levels but the mother–young relationship, which is crucial for the offspring's survival, has not been investigated in large wild mammals. We compared the establishment of the mother–young relationship at birth and during the first week of life and the morphological development of the young in red deer, *Cervus elaphus*, sika deer, *Cervus nippon*, and their hybrids (male *nippon* × female *elaphus*). Most mother–young behaviours did not differ between the three groups, showing strong conservation of peripartum behaviours in cervids. In contrast, the behaviour and body size of the hybrid young were similar or tended to be close to those found in the maternal species, suggesting important maternal effects. In addition, hybrid young were more likely to be standing during the first week than young from the other groups, possibly resulting from increased maternal stimulation and/or hybrid vigour. Adult females in the herd were more likely to perform smell-related and agonistic behaviours towards the hybrid young, suggesting potential species recognition issues, which require further investigation. In conclusion, our findings show that hybridization has no noticeable impact on the mother–young relationship, which could partly explain the success of hybridization between the sika and red deer in the wild.

In taxonomy, species are reproductively isolated groups of populations, but may crossbreed if one cause of isolation is removed (Futuyma, 1983). In this context, approximately 10% of species in major faunal groups that have not evolved sufficient reproductive barriers are known to hybridize with other species (Mallet, 2007, 2008). Hybridization may be associated with gene flow (introgression) and be an important evolutionary mechanism (Harrison & Larson, 2014; Schwenk, Brede, & Streit, 2008), contributing to genetic variation and possibly to loss of species (Allendorf, Leary, Spruell, & Wenburg, 2001; Laikre, Schwartz, Waples, & Ryman, 2010; Sakai et al., 2001) or to speciation (Mallet, 2008). Over the past few centuries, humans have largely contributed to this phenomenon by importing various species (e.g. in Australia: Bomford, 1991; and in Europe: Apollonio, Andersen, & Putman, 2010; Di Castri, Hansen, & Debussche, 2012) from their original to new habitats, thus abolishing geographical barriers between species.

Beyond hybridization, introgression implies various key events including interspecific mating, survival and adaptation of hybrid offspring to their environment and, finally, the stable integration of genetic material from one species to the other through successful repeated backcrossing (Baack & Rieseberg, 2007). In mammals, survival of the young depends strongly on the proper establishment of the mother–young relationship (Clutton-Brock, 1991; Nowak, Porter, Lévy, Orgeur, & Schaal, 2000). To ensure survival of the mother's own young, misdirection of maternal investment should be avoided, notably during lactation. Individual recognition of the young is thus crucial for correct allocation of parental care (e.g. in ungulates, Lévy & Keller, 2008; Romeyer & Poindron, 1992), especially in ungulate hider species, in which calves are hidden and mothers periodically return to them (Briefer & McElligott, 2011; Torriani, Vannoni, McElligott, Coulson, & Losos, 2006). Early parental care has an impact on growth, sexual and social behaviours in adulthood, resulting in differential reproductive success

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(Clutton-Brock, 1991; Lindström, 1999). On the one hand, given that the genotype of hybrid young results from a combination of the genomes of both parental species, an original phenotype due to hybridization may alter recognition cues and thus the establishment of the mother–young relationship (Page, Goldsworthy, & Hindell, 2001), affecting, in turn, offspring survival, growth rate or development (Peripato & Cheverud, 2002). On the other hand, hybridization may result in heterosis or hybrid vigour which increases survival of the young. In the red deer, *Cervus elaphus*, calves with higher heterozygosity are most likely to survive the neonatal period (Coulson et al., 1998). Studying early relationships in a hybridization context is therefore critical to better understand the survival ability of hybrid progeny. Characterizing morphological development is also important as it may reflect differences in parental care, selective pressure and future introgression aptitude of the hybrids (Senn, Swanson, Goodman, Barton, & Pemberton, 2010). For instance, in various species, size is positively correlated with survival and reproductive success (Beauplet & Guinet, 2007; Festa-Bianchet, Jorgenson, & Réale, 2000; Gélin, Wilson, Cripps, Coulson, & Festa-Bianchet, 2016).

Among wild mammals, species in the Cervidae are of major concern for various reasons. While 26 deer species are threatened in the wild (IUCN 2019), others are very common and may even be considered as a pest when overabundant (Nugent et al., 2011). Indeed, some deer species strongly impact local biodiversity through direct and cascading effects due to herbivory selectivity (Côté, Rooney, Tremblay, Dussault, & Waller, 2004). Some of the common cervid species such as the red deer have been widely studied in the wild (e.g. Clutton-Brock, Guiness, & Albon, 1982) and in captivity (Arman, 1974) for several decades, resulting in considerable knowledge of their biology. The sika deer, *Cervus nippon*, has also been well studied (McCullough, Takatsuki, & Kaji, 2008); however, mother–young relationships in this species have rarely been investigated (Fouda, Nicol, Webster, & Metwally, 1990). The sika deer is an invasive species from Asia that is spreading in Europe and has become common in areas usually inhabited by the red deer, leading to conservation issues (McCullough et al., 2008). Indeed, both species are closely related polygynous species that are naturally allopatric but do hybridize when populations become sympatric (Senn & Pemberton, 2009). In Scotland, when sika and red deer populations are found together, the percentage of red deer individuals with sika genetic markers generally remains at a low level (6.9%) but may reach 43% in some areas (Senn & Pemberton, 2009), suggesting that if reproductive barriers remain, they are not absolute. Interestingly, the same study failed to find any F1 hybrids, suggesting that hybridization is rare but not without consequences.

The aim of our study was to test the hypothesis that the establishment of the mother–young relationship differs between red and sika deer and their hybrids. Female red deer were inseminated with sika deer semen to generate hybrid gestations, according to the preferred direction of the introgression between the two species (sika deer male x red deer female, Senn & Pemberton, 2009). We then compared the establishment of mother–young interactions at birth and during the first week of life as well as the morphological development of the young in both species and their hybrids.

METHODS

Animal Housing and Reproduction

In 2013–2015, interactions between red deer mothers giving birth to hybrid calves (sika x red deer, 'ELANIP' group, $N = 9$) were monitored and compared with those of sika and red deer mothers giving birth to young from their own species ('NIP', $N = 8$ and 'ELA' groups, $N = 19$, respectively) at the Réserve Zoologique de la Haute-Touche (RZHT, 46°53′N, 1°04′E), Muséum National d'Histoire Naturelle, Indre, France. Red and sika deer herds at RZHT live in semiwild conditions and have historically been kept in separate areas. We performed handling and training of deer in dedicated facilities connected to these areas. Deer were trained regularly from a young age by positive reinforcement to reduce stress associated with the various procedures involved in the present experiment. The three groups were separated in different enclosures (ranging from 0.8 to 1.4 ha) with a density of 10–12 females/ha. The paddock vegetation included mostly grass, *Carex* and thistle on which the deer could freely graze. A shaded area with trees was available in each paddock. The deer also received a commercial diet daily (Browser Maintenance 5654, Mazuri, Witham, Essex, U.K.) and ad libitum hay and had free access to water. Mothers and their young were marked individually with coloured collars. Females were weighed in a separate facility using a dedicated weighing scale. Female red deer weighed 103–128 kg (mean ± SD: 113 ± 7 kg) and female sika deer 35–49.5 kg (mean ± SD: 42 ± 4 kg).

To control the timing of parturition, oestrus synchronization was performed on red deer females (which had been trained for medical examinations in a dedicated deer crush). Oestrous cycles were synchronized in all the female red deer by inserting intravaginal sponges (2×45 mg, Intervet Schering-Plough Animal Health, Angers, France) filled with fluorogestone acetate (Wyman, Charlton, Locatelli, & Reby, 2011). After 8 days, cloprostenol (75 μg; Estrumate, Intervet Schering-Plough Animal Health, Beaucouzé, France) was injected. Sponges were removed on day 12 and females were injected with 400 UI of pregnant mare serum gonadotropin to induce oestrus and ovulation. Both ELA and NIP groups were then presented to their conspecific males ($N = 2$ and 3 for ELA and NIP, respectively) and bred naturally. To produce hybrids, hinds from the ELANIP group were inseminated by minimally invasive laparoscopy following a similar oestrus synchronization protocol to Wyman et al. (2011). Hinds were fasted 24 h before anaesthesia which was induced by an intramuscular injection of Zoletil (tiletamine 0.5 mg/kg – zolazepam 0.5 mg, Virbac, France) and xylazine (1.5 mg/kg). An endotracheal intubation was performed to maintain anaesthesia using isoflurane (Laboratoires Belamont, Paris, France) and the abdominal region was shaved and prepared for the laparoscopy. Insemination took place 50 h after sponge removal and was performed with pooled frozen/thawed semen from three male sika (100×10^6 spermatozoa/insemination) using an ovine insemination gun (IMV, L'Aigle, France) under minimally invasive laparoscopy examination. Trocart site closure was performed with Vicryl (Ethicon, Johnson & Johnson, Intl., Bridgewater, NJ, U.S.A.) suture. Anaesthesia was reversed by treatment with Yohimbine (1 mg/kg IM), and endotracheal intubation was removed at head-up of the animal. No complications or adverse effects were observed during or following the insemination procedure. Of the 17 females inseminated in 2013, 10 were pregnant at ultrasonography (day 45) and of the nine females inseminated the following year, five were pregnant. During our study, the pregnancy rate was 69% in the NIP group ($N = 13$), 97% in the ELA group ($N = 34$) and 58% in the ELANIP group ($N = 15$). Conception dates were confirmed by weekly monitoring of plasma progesterone, oestradiol and pregnancy-associated glycoprotein (PAGs) levels. Conception dates and gestation lengths from the NIP group were determined by selecting individuals and corresponding data within a larger breeding group. Only females for which it was possible to confirm oestrus (low levels of progesterone and presence of oestradiol, followed by elevation of progesterone and detection of PAGs 3 weeks later) were considered.

Some females were excluded from the experiment for the following reasons. In the ELA group, one calf was born dead. In the ELANIP group, while all the young received proper maternal care at birth, three had welts and were found dead in 2014. For unknown reasons, a few females in the ELA and NIP groups left their young uncared for at birth: these were three primiparous (two red deer and one sika deer) and one multiparous sika deer females. Also, two females (one in the ELANIP group and one in the ELA group) that gave birth to twins were excluded from analysis because twins in nature are very rare and these twins might have resulted from the oestrus synchronization and artificial insemination; in addition, multiple births may affect parameters such as mother–young behaviours, gestation length and milk production as reported in the cow, *Bos taurus* (Cady & Van Vleck, 1978; Price, Martinez, & Coe, 1985).

We determined the sex and measured body mass (2014–2015), mandible length and leg length (in 2015) of calves, in the enclosure within the first 24 h after birth (calves were caught when sleeping during the rest period) and in a separate facility at weaning. Calves were artificially weaned when the mean age of the young within a group reached 100 days, by removing them from their mothers and housing them in a separate barn with access to small paddocks for a 3-month period.

Behavioural Observations

We observed mother–young interactions in 55 dyads from late May to September. Behaviours of the young and the mother (defined in Table 1) were collected using both focal and scan sampling. The first 2 h after parturition were videotaped and the latency, occurrence and duration of behaviours were determined using J-Watcher 1.0 (Blumstein, Daniel, & Evans, 2006). Data available for early mother–young behaviours at parturition were based on 19 ELA females, mean age 6.3 years, including seven primiparous and 12 multiparous females; nine ELANIP females, mean age 5.6 years, including five primiparous and four multiparous females; and eight NIP females, mean age 4.5 years, including four primiparous and four multiparous females. Then, in the first week after birth, presence/absence of behaviours was recorded every 15 min from 0600 to 1200 and from 1400 to 2200 hours, leading to a total of 7647 sightings. In addition, 212 focal sampling sessions were conducted when the dyad was interacting at least once a day during the first week. The data collected during the first week postpartum were from 2015 only.

Statistical Analyses

We analysed behaviours during the first 2 h postpartum and mass gain using linear models with Gaussian or Poisson error distribution. As we had repeated observations of the same individuals, for behaviours and measurements recorded during the first week we used linear mixed models with binomial distribution to avoid any bias due to pseudoreplication. For multiple comparisons between categories, we used Tukey's post hoc test ('library(multcomp)', Hothorn, Bretz, & Westfall, 2008). Because the independent variables are centred and standardized, the value of the estimate indicates the importance of its effect on the response variable for simple variables and interactions (Schielzeth, 2010). Some morphometric measurements of young were not taken at birth and behaviours of some females were recorded for less than 2 h. In these cases, only the latency was used. Sample sizes for each test and for each group are specified in the Results as they depend on the variable of interest. We controlled for factors known to affect behaviours and mass gain, such as age (mother in years and young in days), body mass, sex of the young and intercapture interval by including them as fixed factors. As we only aimed at controlling for the effect of intraspecific variability in the mother's body mass, we used centred values calculated separately for each group. As growth rates are typically size dependent (Hector & Nakagawa, 2012), we also accounted for the size of the young at first capture. All analyses were performed with R version 2.14.1 (R Foundation for Statistical Computing, Vienna, Austria) and user interface Rstudio, version 0.97.551 (Rstudio Integrated Development Environment, Boston, MA, U.S.A.). We used backward stepwise elimination of nonsignificant variables, leading to the minimal adequate model (Crawley, 2007; Zuur, Ieno, Walker, Saveliev, & Smith, 2009).

Ethical Note

In line with European and French regulation on animal experimentation, experimental procedures were approved under reference 01697.02 by the French Research ministry after ethical evaluation (Comité d'Ethique en Experimentation Animale N° 68, Cuvier). One parturient sika deer female was found with a large mammary gland haematoma 10 days after parturition in the enclosure. She was removed from the group to receive veterinary care from the RZHT veterinary service. On the decision of the animal welfare group in charge of the experiment, the male calf was euthanized by the veterinary service. The mother recovered fully from the injury after drainage of the haematoma followed by a 3-week period of medical supervision.

RESULTS

Gestation and Morphometry at Birth

The NIP group had a shorter gestation (219 ± 3 days, $N = 7$) than the ELA group (234 ± 4 days, $N = 13$), while the ELANIP group had

Table 1
Behavioural variables recorded during our observations

	Focal sampling 2 h 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 s) Total duration of teat searching (exploring inguinal area) Total duration of suckling Total duration of standing	Suckling Standing Distance to mother (> or < 2 m)	Duration of mother–young interaction Duration of suckling
Mother	Duration of labour Latency to first licking Total duration of licking No. of mouth openings Latency to eat placenta Total duration of eating placenta	Licking	Duration of licking
Other females	No. of sniffing events No. of kicking events		

an intermediate value (226 ± 4 days, $N = 12$, $P < 0.001$) when controlling for the sex of the young. Females that had a male calf tended to have a longer gestation than those that had a daughter although this was not significant (difference of 2.1 ± 1.2 days; $P = 0.099$). Time of birth ($P = 0.24$) and sex ratio ($P = 0.56$) did not vary significantly between ELANIP ($N = 6$), ELA ($N = 16$) and NIP ($N = 10$) groups.

Morphometric measurements of young at birth differed significantly between the three groups. The ELANIP group was intermediate in terms of body mass, leg and mandible lengths between the ELA and NIP groups (Tables 2, 3, Appendix Table A1, Fig. 1). Males were generally heavier than females at birth (Table 2, Appendix Table A1).

Mother–Young Relationship

Maternal behaviours

At parturition. We found no significant difference between groups in the duration of labour (22 ± 21 min, mean ± SD; $P = 0.82$; Appendix Table A2, Fig. 2a), in the latency (43 ± 58 s, mean ± SD; $P = 0.22$; Appendix Table A2, Fig. 2b) and duration of licking (57 ± 10 min, mean ± SD; $P = 0.95$; Appendix Table A2, Fig. 2d) and in the latency to eat the placenta (89 ± 21 min, mean ± SD; $P = 0.40$; Appendix Table A2, Fig. 2c). Nevertheless, ELANIP mothers spent more time eating the placenta than the ELA group ($P = 0.040$; Appendix Table A2, Fig. 2e). ELANIP mothers opened their mouth more often than ELA and NIP mothers ($P < 0.001$; Appendix Table A2, Fig. 2f).

We generally found no significant difference between male and female young. However, labour tended to last longer for males ($P = 0.052$). Age did not affect maternal behaviours at parturition, but experience did: primiparous females spent more time giving birth ($P = 0.020$). Parity also affected the number of mouth openings ($P = 0.024$): primiparous females did this more in the ELA group but less in the ELANIP group than multiparous females. No difference was observed for mouth opening in the NIP group. Other maternal behaviours were not affected by parity.

ELANIP calves were more frequently sniffed ($P < 0.001$; Fig. 3a) and kicked ($P < 0.001$; Fig. 3b) by other mothers in the group than nonhybrids during the first 2 h after parturition.

First week after parturition. During the first postpartum week, ELANIP mothers spent more time licking their young than NIP and ELA mothers (Table 4, Appendix Table A2). Licking occurrence generally decreased with increasing age of the young and heavier mothers were more likely to lick their young (Table 4). Sex and age of the young, as well as parity status of the mother, did not affect maternal behaviours during the first week.

Young behaviour

At parturition. We found no significant difference between groups in the latency to the first standing attempts ($P = 0.07$; Appendix Table A2, Fig. 4a), in the duration of standing ($P = 0.53$; Appendix Table A2, Fig. 4e) and in the duration of teat searching ($P = 0.35$; Appendix Table A2, Fig. 4d). However, ELANIP and ELA calves stood quicker ($P = 0.006$; Appendix Table A2, Fig. 4b) and found the teat earlier than NIP calves ($P < 0.001$; Appendix Table A2, Fig. 4c). ELANIP calves spent more time suckling than NIP calves, but ELA neonates did not differ from the other two groups ($P = 0.043$; Appendix Table A2, Fig. 4f).

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

First week after parturition. The calf's sex and the parity status of its mother had no effect on its behaviour. Duration of suckling was not significantly different between the three groups (Table 4, Appendix Table A2).

Suckling occurred more often for heavier than lighter mothers (Table 4). Suckling duration decreased with time and the effect of age on standing and licking activities varied between groups: ELANIP young were more likely to be standing than ELA and NIP calves (Table 4, Appendix Table A2). In all groups, young were closer to their mother when they were standing ($P < 0.001$). Time spent standing increased significantly only in ELANIP and ELA young (Table 4).

Young that were quicker to stand gained more mass ($P = 0.009$). Other early behaviours, however, did not significantly affect mass gain ($P > 0.05$).

DISCUSSION

To our knowledge, this is the first study to characterize the establishment of mother–young relationships and the growth of interspecific hybrid young in large wild mammals while comparing them with both parent species. Overall, more than 40% of the mother-young behaviours (eight of 18) investigated did not differ significantly between groups. Behaviour and body size of the hybrid young were similar or tended to be close to those of the maternal species, suggesting strong genetic impact and/or effects of the maternal environment. In addition, hybrid young were more likely to be standing during the first week than those from the other groups, possibly resulting from increased maternal stimulation and/or hybrid vigour. Our study also showed that other adult females in the herd were more likely to perform smell-related and agonistic behaviours towards hybrid than other young, suggesting potential species recognition issues, which require further investigation. Altogether, this study demonstrates that hybrid young are viable and the crucial mother–young relationship is not adversely affected.

Table 2
Effects of the group on body mass, leg and inferior mandible length at birth

Measurements	No. of individuals	Fixed effects		
		Group compared to ELANIP	Sex of young compared to female	Mother's mass (kg)
Birth mass (kg)	65 54[a]	ELA: 0.9 (0.3) NIP: -5.7 (0.3)	Male: 0.7 (0.2)	*0.05 (0.03)*
Leg length at birth (cm)	24	ELA: 1.8 (0.6) NIP: -6.7 (0.5)	NA	0.09 (0.03)
Mandible length at birth (cm)	24	ELA: 1.8 (0.4) NIP: -3.1 (0.3)	NA	*0.03 (0.02)*

ELANIP: hybrid sika deer × red deer; ELA: red deer; NIP: sika deer. NA: not applicable. Italic indicates nonsignificant variables not included in the final model. Estimates (SD) are based on linear models.

[a] No. of individuals = 32 when including mother mass as a random effect in the model.

Table 3
Effects of the group on body mass, leg and inferior mandible length at weaning

Measurements	*N*	Fixed effects			
		Group compared to ELANIP	Mother's 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)	*0.06 (0.04)*	0.84 (0.36)	0.04 (0.01)

ELANIP: hybrid sika deer × red deer; ELA: red deer; NIP: sika deer. Italic indicates nonsignificant variables not included in the final model. Estimates (SD) are based on linear models.

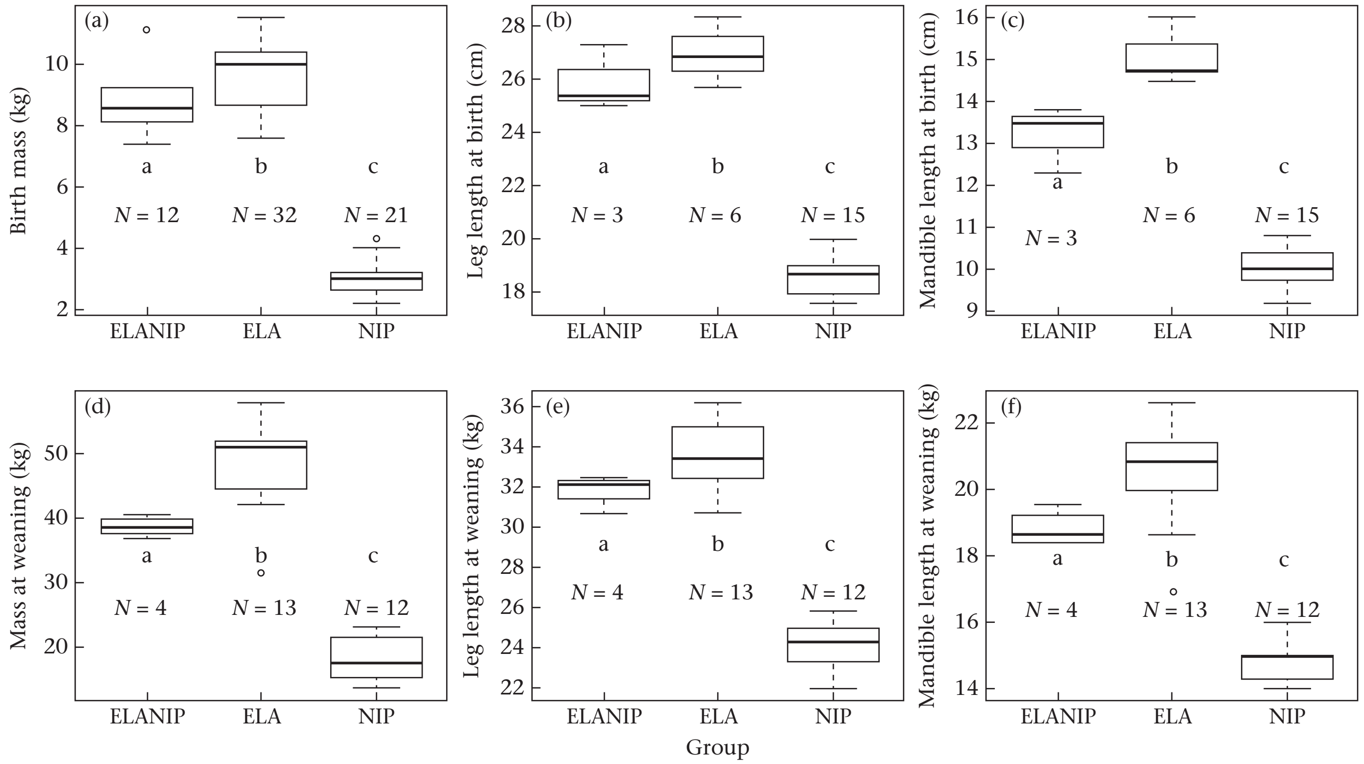

Figure 1. Box plots for (a) mass, (b) leg length and (c) mandible length at birth and (d) mass, (e) leg length and (f) mandible length at weaning (age at weaning: 102 ± 12 days) according to group: ELANIP: hybrid sika deer × red deer; ELA: red deer; NIP: sika deer. *N* = number of young. Different letters indicate significant differences at $P < 0.05$. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers.

Similarity of Peripartum Behaviour

The birth process and the subsequent mother–young interactions were similar among the three groups. Females expressed crucial behaviours such as standing, licking and suckling and showed a strong attraction for amniotic fluids, calves being cleaned immediately after birth. The expression of maternal behaviour in red deer was similar to that previously observed and calves were readily accepted at first sucking (Arman, 1974; Arman, Hamilton, & Sharman, 1978; Clutton-Brock et al., 1982). However, studies documenting later interactions between red deer mothers and calves are lacking, thus preventing further comparisons. In sika deer, Fouda et al. (1990) also reported a short latency for first standing and suckling after birth. In addition, these previous studies (Clutton-Brock et al., 1982; Fouda et al., 1990) documented a marked reduction in suckling bouts and suckling duration between birth and 1 week of life as observed in our study.

We found few effects of parity on maternal behaviours. The strongest effect was observed on labour duration, primiparous females taking longer to deliver their calf. This effect of maternal experience on labour duration has been previously reported in various species including sheep, *Ovis aries* (Dwyer & Lawrence, 2005) and can be related to the less mature physiological processes of parturition in primiparous females (Meurisse et al., 2005; Nowak et al., 2000).

Our results are largely in accordance with previous descriptions of early maternal and calf behaviours of the red and sika deer. Interestingly, we previously documented appropriate mother–young behaviour in a sika calf born from a red deer mother, through in vitro fertilization and interspecific embryo transfer and gestation (see Locatelli et al., 2008). This result further demonstrates that there is no behavioural incompatibility between these species as suggested by their very close phylogenetic relationship (Fernández & Vrba, 2005; Polziehn & Strobeck, 1998) and similar reproductive tactics (Geist, 1998). Indeed, in precocial species, such as most ungulates, the mother–young relationship is characterized by a small litter of fully developed young capable of following the mother shortly after birth. The rapid development of mother–young recognition, which allows

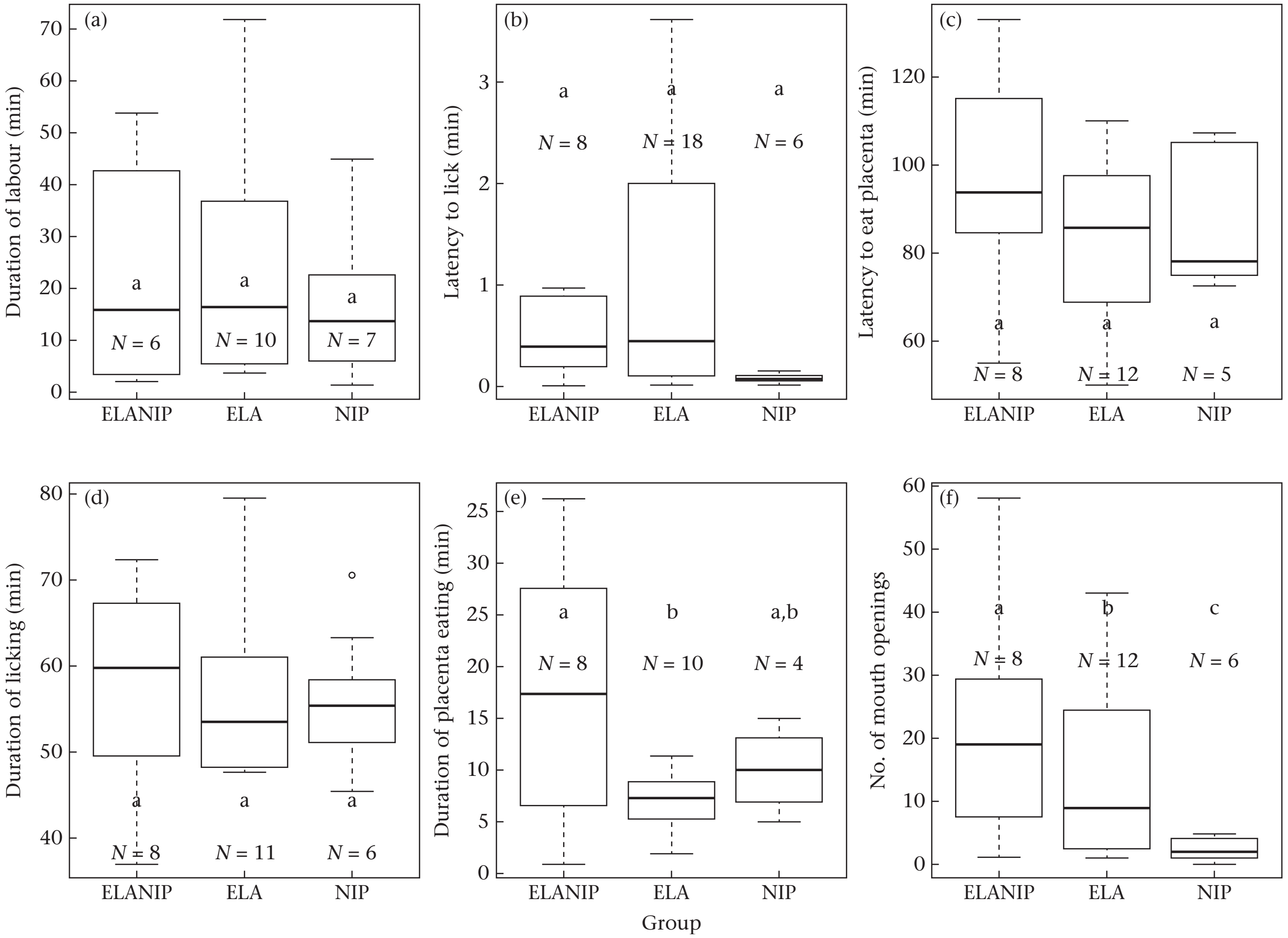

Figure 2. Box plots for (a) duration of labour, (b) latency to lick, (c) latency to eat placenta, (d) duration of licking, (e) duration of placenta eating and (f) number of mouth openings for mothers in each group: ELANIP: hybrid sika deer × red deer; ELA: red deer; NIP: sika deer. *N* = number of females. Different letters indicate significant differences at $P < 0.05$. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers.

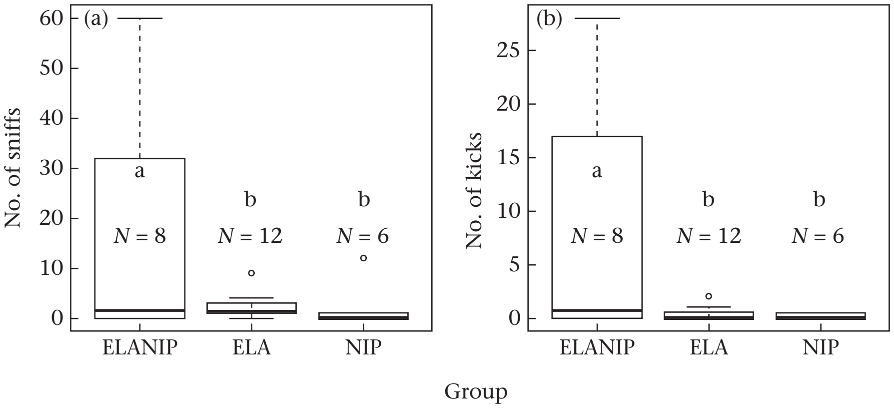

Figure 3. Box plots for (a) number of sniffs and (b) number of kicks directed towards the young during the first 2 h after birth by females other than its mother in each group: ELANIP: hybrid sika deer × red deer; ELA: red deer; NIP: sika deer. *N* = number of young. Different letters indicate significant differences at $P < 0.05$. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers.

exclusive care, is a main feature of these species. In addition, some species, including sika and red deer, show a hiding strategy, that is, during the first few days postpartum offspring hide in the vegetation between two suckling episodes to avoid detection by predators (Lent, 1974; Nowak et al., 2000).

Together, these results suggest that the mother–young relationship is well conserved in cervid species and ungulates in general because of strong evolutionary and ecological constraints (Lent, 1974; Clutton-Brock, 1991) that trigger, both in the mother and in the young, the rapid establishment of a reciprocal bond

Table 4
Occurrence of maternal licking, and suckling–standing activities in the young during the first week after birth in each group

Behaviour	Fixed effects					
	Group compared to ELANIP	Age of young (days)	Mother's mass (kg)	Age of mother (year)	Group*Age of young	Group *Age of 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)	*0.03 (0.16)*	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

ELANIP: hybrid sika deer × red deer; ELA: red deer; NIP: sika deer. $N = 7451$ sighting on 20 individuals. Italic indicates nonsignificant variables not included in the final model. Estimates (SE) are based on linear mixed models (binomial distribution).

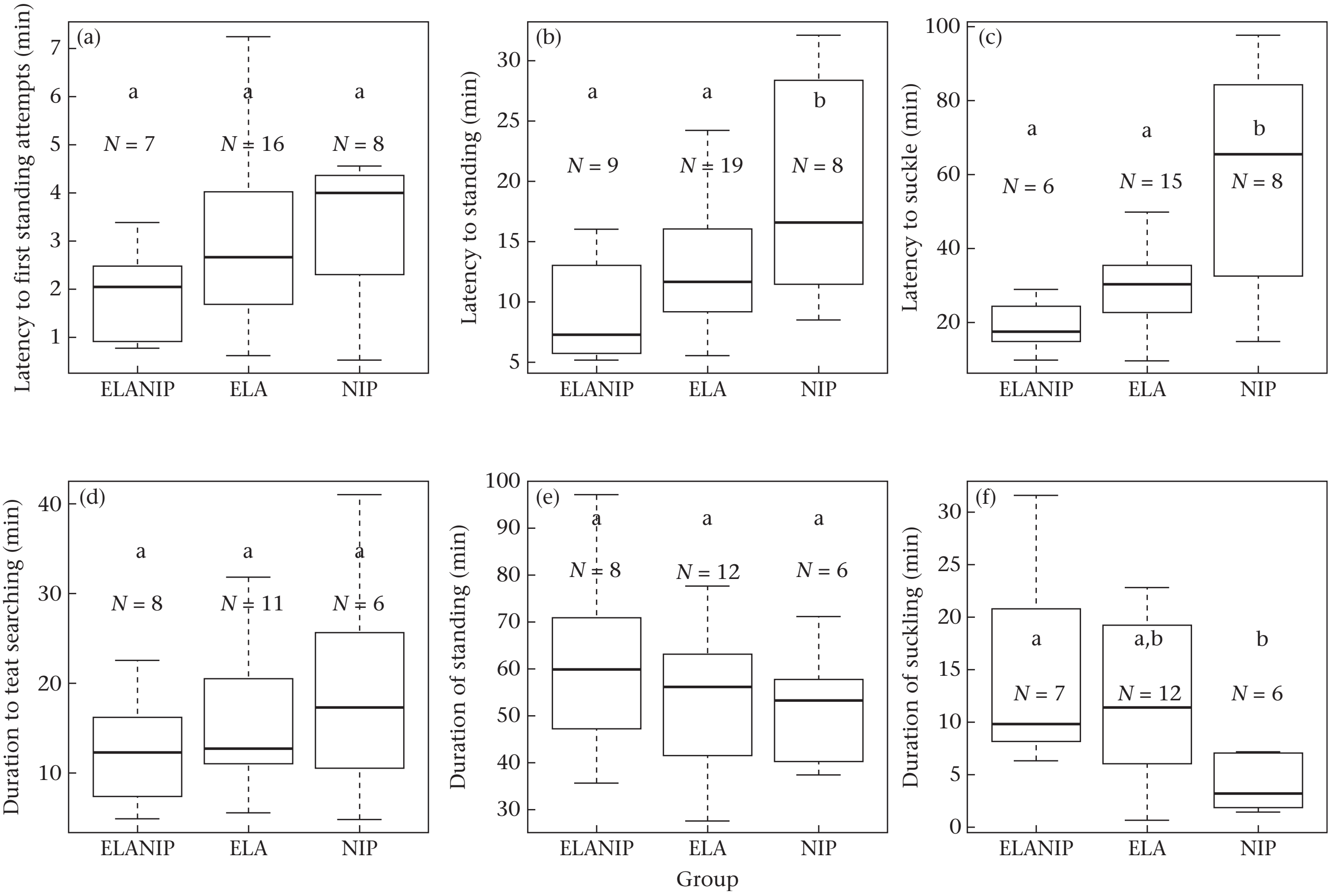

Figure 4. Box plots for (a) latency to first standing attempts, (b) latency to stand, (c) latency to suckle, (d) duration of teat searching, (e) duration of standing and (f) duration of suckling within 2 h after birth according to group: ELANIP: hybrid sika deer × red deer; ELA: red deer; NIP: sika deer. N = number of young. Different letters indicate significant differences at $P < 0.05$. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range.

after birth. Maternal care in mammals is associated with substantial costs, including the expenditure of energy for milk production and the increased risk of predation resulting from the presence of conspicuous neonates also limiting their mobility (Clutton-Brock, 1991). Habitat shifts can be observed in females around parturition and potential predation pressure may override increased nutrient demands during late stages of pregnancy (Berger, 1991). Ensuring the survival of her offspring is thus of prime importance for the mother (Trivers, 1972). For the young, it is a question of individual survival, as the mother is the main source of food until weaning. The mother's milk not only provides the energy necessary for her offspring's survival and growth but also transmits immunity against pathogens through ingestion of colostrum and milk (Grindstaff, Brodie, & Ketterson, 2003). Consequently, little variability in crucial peripartum behaviours is expected among cervids.

Effect of Hybridization

The gestation lengths we observed for both sika and red deer are in accordance with previous findings (Asher, 2007; Matsuura, Sato, Suzuki, & Ohtaishi, 2004). When compared with the parent species, sika x red deer hybridization was associated with a strong effect on gestation length and calf birth mass. Intermediate gestation length of hybrids (226 days versus 219 days in sika and 234 days in red deer) allowed the birth of healthy calves slightly smaller than red deer calves but far bigger than those of sika deer. Interestingly, phenotypic traits of the hybrid young at birth were extremely close to those of red deer, making it difficult to distinguish between hybrid and red deer calves when they were under the mother. Persisting differences in size observed at birth and at weaning are likely to remain in adults as found by a previous study (Senn et al., 2010).

To our knowledge, few consistent data on gestation length or birth weight are available for hybridization between red and sika deer. Hybridization may lead to a shorter gestation and lighter calf birth weight compared to the maternal species if the females are inseminated by a male of a smaller species. For instance, a study focusing on hybridization between hind wapiti, *C. elaphus manitobensi*, and sika also reported a decrease in weight of hybrid progeny at weaning compared with wapiti (Willard et al., 1998). Smaller offspring are expected to consume less milk, reducing the cost of weaning for the mother. Indeed, lactation is the costliest part of reproduction (Oftedal, 1985) and weaning offspring can have more effect on future reproductive success than a shorter duration of lactation (Gélin, Wilson, Coulson, & Festa-Bianchet, 2015). As the probability of survival is generally higher for calves born earlier in the year (Clements, Clutton-Brock, Albon, Pemberton, & Kruuk, 2011), a shorter gestation, and thus an earlier birthdate, may also increase their fitness. This could then decrease the mother's reproductive effort, suggesting a possible advantage for mothers to produce hybrids in some situations. However, breeding with males of a bigger species may cause complications during labour and would then only be expected if hybrids provide a substantial increase in reproductive success compared to nonhybrids to offset the higher reproductive cost for the mother (Moore & Littlejohn, 1989).

Hybrids stood quicker than sika calves at birth and on average spent more time standing in the first week than calves from the other two groups. These differences probably reflect genetic differences as both hybrid and red deer calves experienced identical environmental conditions. This finding supports a previous study on hybrid vigour relating to standing behaviour in cervids (Endicott-Davies, Barrie, & Fisher, 1996). In addition, young that stood quicker gained more mass, possibly increasing future survival and reproductive success (Clutton-Brock, Major, Albon, & Guinness, 1987; Festa-Bianchet et al., 2000). Contrary to what was suggested in a previous study (Senn et al., 2010), the present results do not indicate that hybrid offspring might be less viable than those of the parent species. Furthermore, ungulates are a precocial species in which social imprinting can occur, as shown in sheep and goats, *Capra hircus* (Kendrick, Hinton, Atkins, Haupt, & Skinner, 1998, 2001). The young thus form a preference for their adoptive species, which may last until adulthood in the context of sexual behaviour. Thus, it can be hypothesized that male and female hybrid deer will look for red deer hinds or stags, respectively, as sexual partners, thereby reinforcing the process of introgression.

Some aspects of maternal behaviour were also affected by hybridization. Red deer mothers giving birth to a hybrid calf spent longer eating the placenta in the first 2 h after parturition than those with a neonate of their own species. This was unexpected as the size of the placenta is thought to be proportional to calf birth weight. Whether this longer duration was linked to differences in placenta size or appetence factors requires further data. Red deer mothers giving birth to hybrids also opened their mouth more at parturition. Mouth opening by the mother may reflect flehmen-like behaviours favouring the transfer of odours into the vomeronasal organ (Døving & Trotier, 1998). However, unlike a typical flehmen response, no curling back of the upper lip was observed. Mouth opening was more similar to 'sniff-yawning' behaviour, reported to occur in female bovines in the context of parturition (Halder & Schenkel, 1972; O'brien, 1982). The behaviour we observed, specifically shown when the mother was licking and eating the placenta, may indicate an olfactory-guided activity and potentially reflects some differences in the chemosensory characteristics of the hybrid placenta (O'brien, 1982; Schaal, Coureaud, Marlier, & Soussignan, 2001). This possibility requires further investigation. In addition, mothers of hybrids licked their offspring for longer than mothers in the other groups during the first week after parturition, probably reflecting a reaction to novelty or unfamiliarity (Krames, 1970). Hybrid young were also sniffed and attacked more often by the other mothers in the herd suggesting that species recognition could be mediated through olfaction. Together, these findings may suggest potential species recognition issues in a hybridization context, but further investigations are required to confirm this hypothesis. Our observations were done with semiwild deer, which is likely to have affected some of our results. One important difference is linked to the density of parturient females within an enclosure. In the wild, red deer females isolate themselves for parturition but complete isolation for parturient females in the present study was clearly not possible. Thus, it is likely that aggressive behaviour by other parturient females towards alien young in the ELANIP group might have resulted from the semiwild living conditions and would not be observed in the wild. Similarly, these conditions might have made interactions between mother and young more likely. Finally, the ad libitum resources might have improved both development of the young and survival rates. Nevertheless, living conditions in the present study were identical between groups, confirming the effects of hybridization observed.

In conclusion, this study is one of the few providing detailed information about gestation length, the early mother–young relationship and morphometric measurements in an interspecific hybrid of a large mammal. We found that hybridization had no noticeable impact on the mother–young relationship, allowing survival of a potentially more vigorous hybrid young with phenotypic traits closer to those of the maternal species. We have provided new evidence for the risk of introgression of sika genetics into the red deer, allowing a better understanding of the success of interspecific hybridization in the wild and bringing possible insights for management of hybrid populations.

Author contributions

U.G. conceived the behavioural protocol, performed the field study and analysed the data. M.K., F.L., Y.L. and R.N. conceived the project and secured the funding. V.dB. contributed to fieldwork and to video analysis. Y.L. performed the experiment. All authors contributed to writing the manuscript.

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Appendix

Table A1
Morphometric characteristics of young born from female red deer and sika deer that gave birth to offspring of their own species (ELA and NIP, respectively), and of female red deer that gave birth to hybrid young resulting from insemination by sika deer semen (ELANIP) in 2014–2015

Variables	Years	ELANIP	ELA	NIP
Body mass at birth (kg)	2014	8.4 ± 0.7 (7.4–9.2); 5 females: 8.1 ± 0.6 (7.4–8.7); 3 males: 9.0 ± 0.3 (8.6–9.2)	9.5 ± 1.0 (7.6–11.5); 11 females: 9.1 ± 1.2 (7.6–11.5); 8 males: 10.0 ± 0.5 (9.0–10.5)	2.7 ± 0.4 (2.2–3.2); 3 females: 2.7 ± 0.2 (2.6–3.0); 3 males: 2.7 ± 0.5 (2.2–3.2)
	2015	9.1 ± 1.4 (8.0–11.1); 3 females: 8.5 ± 0.6 (8.0–9.2); 1 male: 11.1	9.9 ± 1.2 (7.8–11.5); 6 females: 9.5 ± 1.2 (7.8–11.3); 7 males: 10.2 ± 1.1 (8.0–11.5)	3.2 ± 0.5 (2.5–4.3); 7 females: 3.1 ± 0.4 (2.5–3.6); 8 males: 3.3 ± 0.6 (2.5–4.3)
	2014–2015	8.7 ± 1.0 (7.4–11.1); 8 females: 8.2 ± 0.6 (7.4–9.2); 4 males: 9.5 ± 1.1 (8.6–11.1)	9.7 ± 1.1 (7.6–11.5); 17 females: 9.3 ± 1.2 (7.6–11.5); 15 males: 10.1 ± 0.8 (8.0–11.5)	3.0 ± 0.5 (2.2–4.3); 10 females: 3.0 ± 0.4 (2.5–3.6); 11 males: 3.1 ± 0.6 (2.2–4.3)
Leg length at birth (cm)	2015	25.9 ± 1.2 (25.0–27.3); 2 females: 25.2 ± 0.3 (25–25.4); 1 male: 27.3	26.9 ± 0.9 (26.0–28.3); 2 females: 26.0 ± 0.4 (25.7–26.3); 4 males: 27.4 ± 0.7 (26.3–28.3)	18.6 ± 0.7 (17.6–20.0); 7 females: 18.6 ± 0.7 (17.6–19.5); 8 males: 18.6 ± 0.7 (17.9–20.0)
Mandible length at birth (cm)	2015	13.2 ± 0.8 (12.3–13.8); 2 females: 12.9 ± 0.8 (12.3–13.5); 1 male: 13.8	15 ± 0.6 (14.5–16.0); 2 females: 14.6 ± 0.1 (14.5–14.7); 4 males: 15.2 ± 0.6 (14.7–16.0)	10.1 ± 0.5 (9.2–10.8); 7 females: 10.0 ± 0.6 (9.2–10.8); 8 males: 10.1 ± 0.4 (9.5–10.8)
Age at weaning (days)	2015	103 ± 5 (95–106; *N*= 4)	99 ± 8 (79–106; *N* = 13)	105 ± 17 (72–130; *N* = 13)
Body mass at weaning (kg)	2015	38.6 ± 1.5 (37.0–40.5); 3 females: 38.5 ± 1.8 (37.0–40.5); 1 male: 39.0	48.9 ± 7.2 (31.5–58.0); 6 females: 45.7 ± 7.7 (31.5–51.5); 7 males: 51.6 ± 5.8 (43.5–58.0)	17.9 ± 3.3 (13.5–23.0); 5 females: 16.1 ± 2.1 (13.5–18.5); 7 males: 19.1 ± 3.5 (14.5–23.0)
Leg length at weaning (cm)	2015	31.9 ± 0.8 (30.7–32.5); 3 females: 31.8 ± 1.0 (30.7–32.5); 1 male: 32.1	33.7 ± 1.6 (30.7–36.2); 6 females: 32.8 ± 1.3 (30.7–34.5); 7 males: 34.5 ± 1.5 (32.3–36.2)	24.2 ± 1.2 (22.0–25.8); 5 females: 23.8 ± 1.1 (22.0–24.8); 7 males: 24.4 ± 1.3 (22.5–25.8)
Mandible length at weaning (cm)	2015	18.8 ± 0.5 (18.4–19.5); 3 females: 18.9 ± 0.6 (18.4–19.5); 1 male: 18.4	20.6 ± 1.6 (16.9 ± 22.6); 6 females: 20.6 ± 1.5 (18.6–22.6); 7 males: 20.6 ± 1.9 (16.9–22.6)	14.8 ± 0.7 (14.0–16.0); 5 females: 14.6 ± 0.5 (14.0–15.0); 7 males: 15.0 ± 0.7 (14.0–16.0)

Means are given ± SD with range in parentheses.

Table A2
Number, latency and duration of maternal and young behaviours at birth in 2014–2015, of female red deer and sika deer that gave birth to young of their own species (ELA and NIP, respectively), and of female red deer that gave birth to hybrid young resulting from insemination by sika deer semen (ELANIP)

Behaviours	ELANIP	ELA	NIP
Other females at parturition[a]			
No. of sniffs	16 ± 23 (*N* = 8 individuals)	2 ± 2 (*N* = 12 individuals)	2 ± 5 (*N* = 6 individuals)
No. of kicks	8 ± 12 (*N* = 8 individuals)	0 ± 1 (*N* = 12 individuals)	0 ± 0 (*N* = 6 individuals)
Mother at parturition			
Duration of labour (min)	22 ± 22 (*N*=6 individuals)	25 ± 25 (*N*=10 individuals)	16 ± 15 (*N*=7 individuals)
Latency to licking (s)	29 ± 23 (*N* = 8 individuals)	62 ± 70 (*N* = 18 individuals)	5 ± 3 (*N* = 6 individuals)
Latency to eat placenta (min)	97 ± 25 (*N* = 8 individuals)	84 ± 19 (*N* = 12 individuals)	88 ± 17 (*N* = 5 individuals)
Duration of licking (min)	58 ± 12 (*N* = 8 individuals)	57 ± 10 (*N* = 11 individuals)	56 ± 8 (*N* = 6 individuals)
Duration of placenta eating (min)	18 ± 13 (*N* = 8 individuals)	7 ± 3 (*N* = 10 individuals)	10 ± 4 (*N* = 4 individuals)
No. of mouth openings	21 ± 19 (*N* = 8 individuals)	14 ± 14 (*N* = 12 individuals)	2 ± 2 (*N* = 6 individuals)
Young at parturition			
Latency to first standing attempts (min)	2 ± 1 (*N* = 7 individuals)	3 ± 2 (*N* = 16 individuals)	3 ± 1 (*N* = 8 individuals)
Latency to standing (min)	9 ± 4 (*N* = 9 individuals)	13 ± 5 (*N* = 19 individuals)	19 ± 9 (*N* = 8 individuals)
Latency to suckling (min)	16 ± 4 (*N* = 6 individuals)	30 ± 10 (*N* = 15 individuals)	60 ± 31 (*N* = 8 individuals)
Duration of teat searching (min)	12 ± 6 (*N* = 8 individuals)	16 ± 8 (*N* = 11 individuals)	19 ± 13 (*N* = 6 individuals)
Duration of standing (min)	61 ± 19 (*N* = 8 individuals)	54 ± 16 (*N* = 12 individuals)	52 ± 12 (*N* = 6 individuals)
Duration of suckling (min)	15 ± 10 (*N* = 7 individuals)	12 ± 8 (*N* = 12 individuals)	4 ± 3 (*N* = 6 individuals)
Mother/young in first week			
Proportion of time that mother spent licking its young	0.12 (*N* = 1512 sightings, 4 individuals)	0.08 (*N* = 2646 sightings, 7 individuals)	0.06 (*N* = 3293 sightings, 9 individuals)
Proportion of time spent suckling by young	0.06 (*N* = 1512 sightings, 4 individuals)	0.05 (*N* = 2646 sightings, 7 individuals)	0.05 (*N* = 3293 sightings, 9 individuals)
Proportion of time spent standing by young	0.19 (*N* = 1512 sightings, 4 individuals)	0.13 (*N* = 2646 sightings, 7 individuals)	0.10 (*N* = 3293 sightings, 9 individuals)

Means are given ± SD. We carried out focal sampling at parturition and scan sampling in the first week.

[a] Behaviour of other females in the group towards the young.

Table A3
Daily proportion and estimated duration of maternal and young behavioural interactions during the first week following birth in 2015 of female red deer and sika deer that gave birth to young of their own species (ELA and NIP, respectively), and of female red deer that gave birth to hybrid young resulting from insemination by sika deer semen (ELANIP)

Variables during first week	All groups	ELANIP	ELA	NIP
No. of daily mother–young interactions	2.5 ± 1.3 (0–7) (*N* = 139 sightings, 20 individuals)	3.7 ± 1.4 (2–7) (*N* = 28 sightings, 4 individuals)	2.6 ± 1.1 (0–5) (*N* = 49 sightings, 7 individuals)	1.8 ± 1.3 (0–4) (*N* = 62 sightings, 9 individuals)
Average duration of mother–young interactions (min:s)	24:12 ± 19:48 (0:23–99:51) (*N* = 217 sightings, 20 individuals)	21:32 ± 19:18 (1:18–99:51) (*N* = 53 sightings, 4 individuals)	29:12 ± 16:59 (1:21–92:21) (*N* = 71 sightings, 7 individuals)	24:10 ± 20:20 (0:23–94:23) (*N* = 93 sightings, 9 individuals)
Proportion of time spent licking during observations	0.33 ± 0:19 (0.00–1.00) (*N* = 217 sightings, 20 individuals)	0.39 ± 0:20 (0.06–0.85) (*N* = 53 sightings, 4 individuals)	0.36 ± 0:19 (0.06–1.00) (*N* = 71 sightings, 7 individuals)	0.27 ± 0:14 (0.00–0.89) (*N* = 93 sightings, 9 individuals)
Proportion of time spent suckling during observations	0.30 ± 0:25 (0.00–1.00) (*N* = 217 sightings, 20 individuals)	0.22 ± 0:17 (0.01–0.82) (*N* = 53 sightings, 4 individuals)	0.23 ± 0:16 (0.00–0.65) (*N* = 71 sightings, 7 individuals)	0.39 ± 0:21 (0.02–1.00) (*N* = 93 sightings, 9 individuals)
Estimated daily duration of interactions (min)	60 ± 30	79 ± 40	75 ± 55	43 ± 30
Estimated daily duration of time spent licking (min)	20 ± 18	31 ± 04	27 ± 20	11 ± 45
Estimated daily duration of time spent suckling (min)	18 ± 27	17 ± 32	17 ± 28	16 ± 58

Means are given ± SD. We made daily observations using 15 min interval scan sampling between 0600 and 1100 hours and between 1400 and 2200 hours and focal sampling.