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Impact of interspecific relations between native red deer *(Cervus elaphus)* and introduced sika deer *(Cervus nippon)* on their rutting season in the Doupovské hory Mts.

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ABSTRACT: The behaviour of sika and red deer during the rutting season is highly variable in relation to vocalization, habitat preference during the rut, and onset and termination of rutting. The red deer is a native species in Central Europe, but the areas where it lives in sympatry with the introduced sika deer have been increasing in the last three decades. Such situation can be found in the Doupovské hory Mts., where sika deer has been intensively spreading. Hybridization between the two species and changes in behaviour are the most important problems. In this study we prove the shift in the rutting period shown by both species. To evaluate the shift in the rutting season, we used a very extensive long-term data set on deer shot within the Military Training Area. These changes occur very slowly, however, and are very difficult to monitor and evaluate in the wild. Based on our results, the timing of the rutting season has converged at the mean rate of 0.62 day per year (rutting season starts later in the red deer and earlier in the sika deer).

Keywords: shooting date; population density; military area; game management

The timing and synchronization of the rut and subsequent period of producing offspring are fundamental determinants of reproduction in seasonal environments (Loe et al. 2005). This phenomenon is most frequently related to the timing of vegetation growth after winter. Synchronization of the rut and birth of the young are usually studied in connection with climate changes (Walther et al. 2002; Coulson 2003; Loe et al. 2005) or female body condition (Stevenson, Bryant 2000). The influence of climate changes on biodiversity and the related influences on phenology and life history traits are generally known (Plard et al. 2014). Animals living at higher elevations or latitudes and species with high plasticity also frequently exhibit adaptations of life history in relation to breeding phenology. Animals living in northern areas or at higher elevations usually have a more synchronized breeding season than do individuals of the same species living at lower elevations or closer to the equator (Loe et al. 2005). In this study we focussed on the timing of rutting season in the red deer (*Cervus elaphus*). Its breeding phenology is dependent on climate conditions. For example, the rut in Europe begins in the west and subsequently shifts towards the east, which is usually explained in relation to the continental climate of the eastern areas. The dependence of the onset of the rut on climate conditions has been demonstrated by Coulson et al. (2003) when in a red deer population on the Isle of Rum, Scotland, a 10-day shift in the onset of the rut occurred in connection with global warming over the period of 30 years. Nowadays the rut in this population begins earlier than in the past. When comparing breeding phenology of deer in France and Norway, Loe et al. (2005) concluded that temperature and the related spring onset of vegetation growth were essential for the timing and synchronization of the rut. Nevertheless, they stated that female weight also plays an important role. The rut and therefore the birth of offspring were more synchronized in Norway than in France. In relation to this, the condition of females in Norway (measured as autumn body weight) demonstrated a notably lower

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range than that of females in France. In France, a female with higher autumn weight produced offspring earlier. Similar results were reported also by Langvatn et al. (2004) in Norway, who also noted higher female ovulation synchronization in higher population densities, albeit with some delay. The latter study also confirmed the generally known fact that older females are the first to enter the rut (i.e. the start of ovulation). It also reported that females that had not ovulated in the previous year (usually as a result of poor condition), subsequently ovulated earlier than did other females of the same age.

The shift in ovulation is, of course, related to the onset of the male rut and their activity which is induced by the female oestrus phase. Male vocalization is therefore usually most pronounced when the females come into their oestrus peak and lasts 4–5 weeks (Clutton-Brock, Albon 1979). Male activity also increases during the rut. They seek out rutting females, change the locations of their standard home territories and join the females. A higher number of males are concentrated near the females. Activity during both day and night is also significantly increased (Kamler et al. 2008; Pépin et al. 2009). The likelihood of being killed by a hunter rises with the increasing male vocalization (Milner et al. 2006). Hunting of the rutting male deer has very deep cultural roots in Central Europe and is a part of the hunting tradition. In Central Europe, the largest numbers of reproductively active deer are shot at the peak of rut (i.e. in the period of most intensive vocalization).

In recent decades, the non-native sika deer (*Cervus nippon*) has been spreading into many areas in Central Europe. It is a species originating from Asia, and it has been significantly expanding its range especially in the Czech Republic, doing so even within the traditional range of the red deer (Bartoš 2009). Sika deer exhibit a high degree of variability in the mating system (Bartoš et al. 1998). The harem system was reported from New Zealand and England (Putmann, Mann 1990), resource-based territories from native areas such as Russia and Japan (Bartoš et al. 2003), and lek territoriality in an introduced population in the Czech Republic (Balmford et al. 1993). The peak rut activity has been recorded to occur between 17 and 19 October in Austria (Bartoš et al. 2003, enclosure area) and during October in the Czech Republic (free ranging population) (Balmford et al. 1993). Intensive growth in the sika deer population influences the condition of forest ecosystems. Forest management authorities pay much attention to measures protecting the stands against damage from animals, and in forestry circles the actual size of the ungulate game population which affects the specific forest ecosystems is debated (Slodičák et al. 2008). Sika deer overpopulation and its influence on the newly colonized environment and on populations of other game species is a problem in many places around the world. The impact of non-native deer overpopulation has been recorded and described in North America (Alverson et al. 1988; Rooney 2001; Russell et al. 2001; Rooney, Waller 2003), Great Britain (Fuller, Gill 2001; Kirby 2001), Europe (Homolka, Heroldova 2003; Schutz et al. 2003) and New Zealand (Stewart, Burrows 1989). The spreading of certain deer species across the world and their influence on the environment are described as very unsettling (Takatsuki 2009)

Competition for food, the related damage to agricultural and forest stands, and especially spontaneous hybridization with the red deer are considered to be the main problematic interactions of the sika deer with the autochthonous species (Bartoš, Žirovnický 1982; Gehle, Herzog 1998; Goodman et al. 1999). Crossbreeding with red deer has been declared one of the main threats (Bartoš 2009; Senn et al. 2010; Biedrzycka et al. 2012), and generally hybridization with autochthonous species is considered to be one of the greatest problems for global biodiversity (Arnold 2004). Hybridization in free-ranging areas has been molecularly demonstrated only at a few sites (McDevitt et al. 2009; Senn et al. 2010), and mainly in Great Britain. Nevertheless, signs of hybridization are becoming increasingly apparent in other areas too.

The aim of this study is to describe changes in behaviour and reproduction phenology in the red deer and sika deer in areas where both species are present. The shift in the rutting season and female ovulation we tried to document could be a sign of hybridization and behavioural changes.

MATERIAL AND METHODS

Study area. Research and monitoring were carried out in the Doupovské hory Mts., north-western Bohemia, Czech Republic. Almost two thirds of the area are used for military purposes (Fig. 1). The Military Training Area (hereinafter referred to as MTA) has a very restricted public access and hiking is entirely prohibited. This has an undeniable influence on the development of game popula-

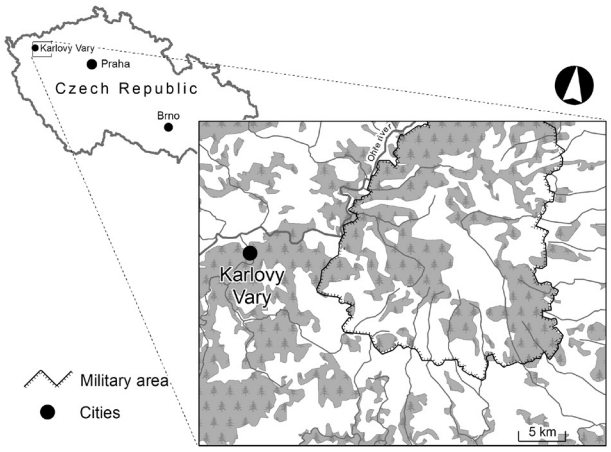

Fig. 1. The Doupovské hory Mts. on a map of the Czech Republic

tions (Lovari et al. 2006). The current extent of the Hradiště MTA is 331.61 km^2, which makes it the largest such area in the Czech Republic and one of the largest in Central Europe. As a result, a number of successive forest development stages and growths of shrubs (dog rose, midland hawthorn, blackthorn) can be found across a large area. In a number of cases, these already have transformed into young deciduous forests (European aspen, sycamore, common ash, wild cherry). Large areas of these growths have very poor access and are sought out by game because of their calmness and large food availability. Plant communities in the Doupovské hory Mts. are represented as follows: coniferous and mixed forests make up 45%; stands undergoing succession 39%; and meadows, pastures, shooting ranges and other areas without tree and bush layer 16%. Elevation of the area ranges from 350 to 934 m a.s.l.

Populations of two sympatric deer species, the red deer and sika deer, are very abundant in the Doupovské hory Mts. In recent decades, sika deer populations have spread spontaneously into the Czech Republic (Homolka, Heroldova 2003), and the Doupovské hory Mts. are a typical example of their new range. Within the MTA, the first mentions of hunted sika deer come from 1968. The two populations significantly affect each other. Increases in numbers (hunted individuals) of the red and sika deer in the last 44 years are shown in Fig. 2. A strong influence of the sika deer on the autochthonous red deer population is the reason why interactions between the introduced sika deer and native species of ungulate game (to which the sika is a new competitor) need to be studied.

Data collection and statistics. The current Hradiště MTA is an integrated hunting ground (Karlovy Vary region in western Bohemia). Since establishment of the hunting ground in 1953, hunting operations and game population management have been carried out by the Karlovy Vary division of the state enterprise Vojenské lesy a statky České republiky, státní podnik (hereinafter referred to as Military Forestry and Lands). In this unified hunting area, detailed data on the hunted large game are collected. Since 2004, the data have been uniformly recorded in the Myslivost (Game Management) software (Karel Janeček, Yamaco Software, Czech Republic). Eleven variables are recorded within 24 hours of each kill: tag number, date of kill, species of game, sex, hunting method, hunter's name, estimated age of the animal, its dressed weight, estimated live weight, trophy, and trophy point score. Hunting is conducted either directly by employees of the Military Forests and Lands or in their presence, and the employees receive financial remuneration for hunted animals and for accompanying a hunt, which ensures precise data recording. The total annual bag fluctuates around an average of 2,000 individuals of hunted red and sika deer in the Hradiště MTA, however, the population has been increasing. The rising number of hunted deer with the representation of hunted males is shown in Fig. 3.

Hunting in the mating season is essential for the total number of hunted males (Fig. 4.). In the last six years, male deer have been hunted also on drive hunts, so hunting outside the mating season is more successful than 10 years ago.

Based on direct observations and evaluation of data on male kills, we used adult male kills as the basic variable determining the peak and timing of the rut. As noted above, the activity of males during the rut increases considerably (Kamler et al. 2008; Pépin et al. 2009) and there is therefore a higher probability of them being killed. We worked on the assumption that males show the

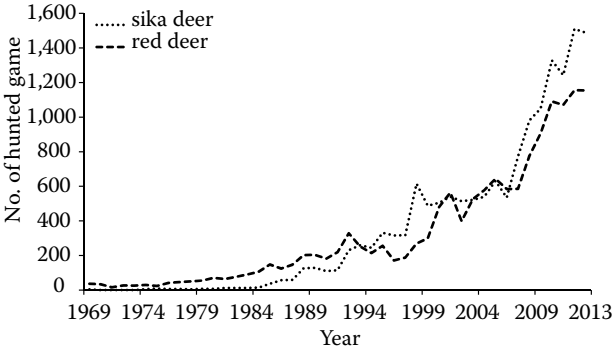

Fig. 2. Numbers of sika and red deer individuals hunted in the study area in 1969–2013

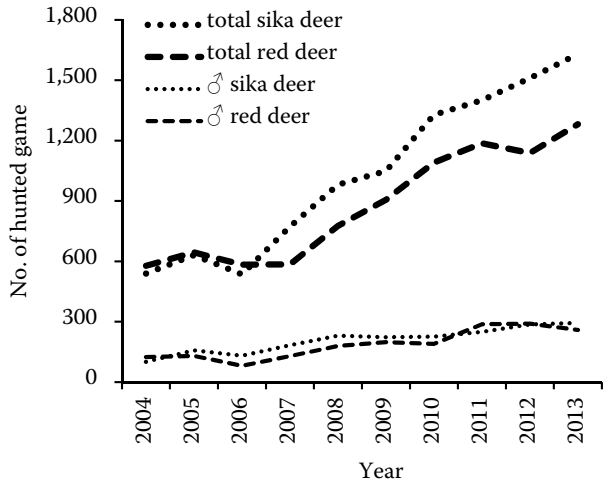

Fig. 3. Increasing population of red and sika deer in the Hradiště MTA over 10 years (2004–2013) – total number of hunted individuals

highest spatial activity during the rut (Georgii, Schroder 1983). At the same time, we assumed that females enter oestrus continuously depending on age and this timing is not affected by short-term weather phenomena (Loe at al. 2005). This is also related with male activity during the rut, which increases with the number of females entering oestrus. We also supposed that the intensity of hunting pressure is constant in the area during the rutting period. Hunting guides continuously accompany hunting guests throughout September and October. Each hunting guide has an assigned part of the hunting area, and after a successful hunt with the hunter, he has to accompany a new hunter the next day. Therefore the number of hunters (and also the level of hunting pressure) is constant over the entire rutting period. Moreover, there were no changes in the age structure of harvested red deer and sika deer during the study period (tested by Kruskall-Wallis ANOVA) and the median value of age was 4–5 years in the red deer and 4 years in the sika deer (except 2004) (Appendix).

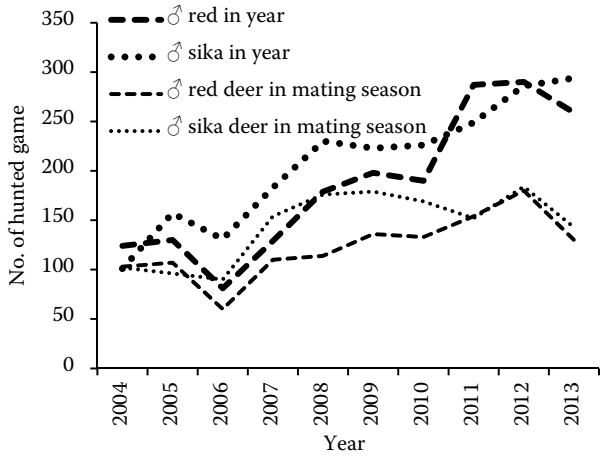

Fig. 4. Numbers of hunted males of the red and sika deer in the Hradiště MTA during 10 years (2004–2013)

Data on deer harvest were gathered during the period 2004–2013 (Table 1). For the purpose of this study, we selected data that fulfilled the following criteria:

- An adult male was hunted.
- The individual type of hunt was applied.
- The hunt took place between 1 September and 31 October. The period was extended in 2012 and 2013 when the deer were hunted also in November, till the first day when no deer were hunted during the individual type of hunt.

Direct observation suggests that in the red deer, the rutting season has shifted to a later part of the year in recent years, while in the sika deer it has shifted to an earlier part of the year. The timing of the rutting season in individual years was determined using hunting data. We assumed that the peak of the rutting season coincided with the mean date of the hunting season.

The potential relationship between the calendar year and the hunting season for each species was assumed to be linear:

$$y = \alpha + \beta x \quad (1)$$

where:
y – date of hunting,
x – calendar year and $\alpha, \beta \in R$ are parameters.

In order to verify the aforementioned assumptions, we tested the null hypothesis that the hunting season for red deer (and for sika deer separately) is independent of the calendar year

Table 1. Number of harvested deer individuals during the mating season

Calendar year	Red deer	Sika deer
2004	103	102
2005	107	96
2006	60	90
2007	110	154
2008	114	176
2009	136	179
2010	133	169
2011	154	152
2012	180	184
2013	130	143

$$H_0 : \beta = 0 \quad (2)$$

against the alternative hypothesis that there is a linear trend

$$H_1 : \beta \neq 0 \quad (3)$$

The parameters of our model were estimated by the least squares method and subsequently a standard statistical analysis was carried out. Let us denote by n the number of x and y measurements carried out, by s the residual standard error of the least squares estimate of Eq. 1,

$$s = \sqrt{\frac{1}{n-2}\sum_{i=1}^{n}(y_i - a - bx_i)^2} \quad (4)$$

where:
a – estimate of α,
b – estimate of β. It can be shown that, assuming (Eq. 2) holds, the test statistic

$$T = \frac{b}{s}\sqrt{\sum_{i=1}^{n}(x_i - \bar{x})^2} \quad (5)$$

has Student's t-distribution with $n - 2$ degrees of freedom. In addition, we can compute the confidence interval for β as

$$b \pm t_{n=2}(\alpha)\, s\sqrt{\frac{1}{\sum(x_i - \bar{x})^2}} \quad (6)$$

and the confidence interval for regression line (Eq. 1) by Seshkin 2011 as

$$a + bx \pm s\sqrt{2F_{2,n=2}(\alpha)}\sqrt{\frac{1}{n} + \frac{(x_i - \bar{x})^2}{\sum(x_i - \bar{x})^2}} \quad (7)$$

To prove the assumption that the hunting and rutting seasons converge, we tested the homogeneity of the two estimates b_1 and b_2, where b_1 is a least square estimate of the slope β_1 in model (1) for red deer and b_2 is an estimate of the slope β_2 for sika deer. That is to say that we tested the hypothesis that they can be considered to be estimates of common β, i.e.

$$H_0 : \beta_1 = \beta_2 \quad (8)$$

against the alternative hypothesis

$$H_1 : \beta_1 \neq \beta_2 \quad (9)$$

It can be shown (Seshkin 2011) that the test statistic

$$H_0 : \beta_1 = \beta_2 \quad (10)$$

where:

b_1, b_2 – are estimates of slopes in two linear models,
n_1, n_2 are corresponding numbers of measurements, and

$$s = \sqrt{\frac{(n_1 - 2)s_1^2 + (n_2 - 2)s_2^2}{n_1 + n_2 - 4}} \quad (11)$$

where:
s_1, s_2 – residual standard errors, have Student's t-distribution with $n_1 + n_2 - 4$ degrees of freedom, assuming that (Eq. 8) holds.

RESULTS AND DISCUSSION

Red deer

Results of the evaluation of model (1) are shown in Table 2. The value of test statistic (Eq. 5) is $T = 3.05$ at 1225 df. The null hypothesis (Eq. 2) can thus be rejected at the significance level 0.01 and the estimate of parameter β takes on a positive value. The 99% confidence interval for β is (0.05, 0.62). The shift in the red deer hunting season to later weeks appears to be statistically significant. Given the relationship between the hunting season and the rutting season, we can also assume a similar shift in the rutting season. A graphic overview of the data and the fitted Eq. (1) are shown in Fig. 5a.

Table 2. Red deer – estimates of linear model parameters

Parameter	Estimate	SD	Test statistic
a	–405.8	222.6	–1.82
b	0.3376	0.1108	3.05

Sika deer

The value of test statistic (Eq. 5) is $T = -2.93$ at 1443 df. The null hypothesis (Eq. 2) can again be rejected at the significance level 0.01, but the estimate of parameter β takes on a negative value this time. The 99% confidence interval for β is (–0.53, –0.03) (Table 3). The shift in the sika deer hunting season (and rutting season) to earlier weeks appears to be statistically significant (Fig. 5b).

Values of β represent the average yearly shift of the mating season. During the study period, the

Table 3. Sika deer – estimates of linear model parameters

Parameter	Estimate	SD	Test statistic
a	849.8	193.6	4.39
b	–0.2822	0.0964	–2.93

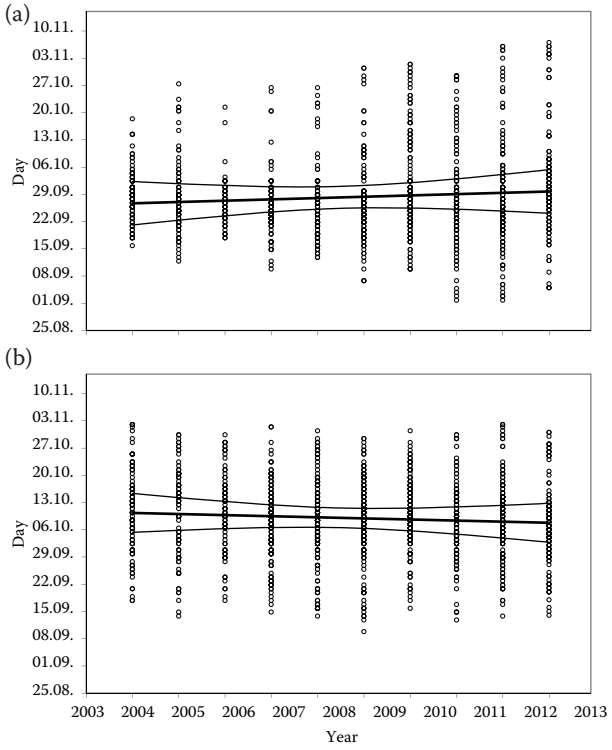

Fig. 5. Hunting season during the period under evaluation of Red deer (a), sika deer (b)

shift was 0.338 days in the red deer and 0.282 days in the sika deer. Our results revealed that the mating season of the red deer shifts by 0.338 days forwards a year, and the mating season of the sika deer shifts by 0.282 days backwards. The mating seasons of the two species thus converge at the mean rate of 0.62 day per year.

Finally, we tested the hypothesis that the estimates of b_1 and b_2 can be considered to be estimates of common β. The value of test statistic (Eq. 10) is $T = 4.24$ at 2668 df. Since the corresponding critical value takes the value of $t_{2668}(0.01) = 2.578$, we are able to reject the hypothesis (Eq. 8) at the significance level 0.01. The convergence of the hunting seasons of the red deer and sika deer appears to be statistically significant.

Strong interactions between sika deer and red deer are described in a number of specialized papers. Wolf and Vavruněk (1975–1976) described how sika deer affected the red deer rut. The situation when a rutting male red deer intensively repels a weaker individual of its own species but ignores a sika deer near its females is commonly mentioned. Suminski (cited in Matuszewski 1988) even stated that the sika deer dominates over the red deer "because it is considerably braver". Matuszewski and Suminski (1984) mentioned that during the rut, young red deer males are attacked by older sika deer. The introduced sika deer is frequently in better physical condition than the domestic deer species, examples of which can be found all over Europe as well as in populations in North America (Armstrong 1980; Butts et al. 1982; Keiper 1985; Richardson, Demarais 1992; Feldhamer, Armstrong 1993). Interspecific relations are mostly based on behavioural traits that are very difficult to observe and which can therefore lead to the opinion that interactions between the local species and the exotic sika deer may not be significant.

Great variability in the sika deer rutting activity has been described across Europe as well as in small areas of its presence (Janiszewski 2007; Matuszewski 1988). The rut usually begins in mid-October and occurs at various intensities over time, frequently being recorded as late as in December (Wolf, Vavruněk 1975–1976; Baskin, Danell 2003). A situation similar to that reported by the latter authors is known from the beginning of development of the sika deer population in the Doupovské hory Mts. In 1996, when the density of the sika deer population was significantly growing and the hunt was becoming increasingly intensive, majority of the rutting-deer hunts were carried out in the second half of October. As contemporary chronicles document, the peak of the sika deer rut in the region was around 25 October. In the Northern Hemisphere, the rutting season of the red deer usually occurs between mid-September and mid-October, and from the start of the rut the deer are intolerant of one another and move to rutting areas with adult females (Ahlén 1965; Clutton-Brock et al. 1982). Throughout the rutting season, the deer are strongly sexually active, spend only less than 10% of time grazing, and are active for essentially the entire day (Kelly et al. 1987). Local chronicles describe the peak of the deer rut in the Doupovské hory Mts. to fall between 20 and 25 September. The aforementioned data indicate that in areas with pure populations there is little overlap between the rutting seasons of the sika deer and red deer.

Visual observations available from the study area suggest gradual changes in the rutting behaviour of both the sika and red deer, especially at sites with increased population densities of the two species. It is often possible to observe a sika deer that does not refrain from vocalizing in the vicinity of a rutting red deer in mid-September. Fifteen years ago, it was almost impossible to encounter the whistling of a sika deer in September. Rutting vocalizations of the sika deer have also undergone a significant change over the decades,

although they have not been studied systematically in this area. The clear whistles that could be heard most frequently in the past have largely been replaced by various sounds that approach bleating and even indications of bugling. Observable changes have also occurred in the timing of the rutting season, thus shifting hunting success during the rut.

As stated above, this is an indirect evidence of extensive hybridization between the native red deer and the introduced sika deer. No direct proof of this phenomenon is available from the area under study, but we can assume that mutual crossbreeding occurs there as well. The fact that the rutting seasons of these species are getting closer highlights the large risk of hybridization, which can lead to gradual extinction of the native species or local population (Allendorf et al. 2001). Our results thus indicate not only a change in genes (which was demonstrated in similar sympatric populations of the sika and red deer in Poland, Biedrzycka et al. 2012), but also a change in behaviour of the two species. It should be mentioned that although the behavioural changes are very inconspicuous and slow, they correspond with previous results which showed that the resulting hybrid is usually considered to be a red deer in "pure conditions" (Bartoš, Žirovnický 1982).

For a number of years, various authors have been warning of the danger of the sika deer being one of the most alarmingly invasive species in Europe (Bartoš, Žirovnický 1982; Bartoš 2009; Daise 2009; Biedrzycka et al. 2012). With the massive spreading of the sika deer in Central Europe, it is necessary to undertake immediate game management measures to stop its expansion and to use all legal means to significantly reduce its population densities.

CONCLUSIONS

When making observations and while hunting, it is possible to detect very interesting divergences from the usual behaviour of the red deer and sika deer. The ideal time for observing such phenomena is during the rutting season, when individuals of both species are easily observable even in the daytime and are highly active. There is no doubt that although the populations of red deer and sika deer are largely interconnected, it is very difficult to understand and describe significant divergences from the normal state. The changes are very gradual, thus making it more difficult to observe minor and even larger changes. Over the past 20 years, an unprecedented expansion of the formerly rare sika deer has taken place in the Doupovské hory Mts. and this species has become the most numerous ungulate game in this area. The influence of this species on other ungulate game species was described in literature already more than 40 years ago (Rowland 1967). The influences described are very extensive in the study area, where large amounts of suitable habitats are available for development of an abundant population. The deepest interactions exist with the red deer – the sika deer is taxonomically closest to this species and crossbreeds with it. Individuals are frequently killed whose species determination is difficult even for experienced gamekeepers and zoologists, and there are other manifestations, too, to confirm crossbreeding. The shift in the timing of the rutting season is such a manifestation which is very striking in comparison with areas inhabited by pure populations of the sika deer and red deer. The local populations of the red deer and sika deer in the Doupovské hory Mts. are, of course, not isolated from their surroundings, and they also communicate with neighbouring abundant populations of the two species. The intensive growth of the sika deer population influences not only other game species, but also the surrounding environment. At a suitable site, even the formerly very scarce sika game can quickly multiply, live covertly and cause significant damage especially to forest stands. Serious research has been carried out since 2009 with the aim to monitor the growth of the sika deer population, its behaviour and its influence on the environment in the Doupovské hory Mts.

Appendix

The shift of the peak of rut could also be a result of changes in the age structure of males (as suggested by one of the anonymous referees). Therefore we also tested differences in the age structure of the harvested deer in different years. We supposed that there were no changes in the age structure of the harvested red deer and sika deer during the study period (tested by Kruskall-Wallis ANOVA) and the median value of age was 4–5 years in the red deer and 4 years in the sika deer (except 2004) (Fig. 6a,b)

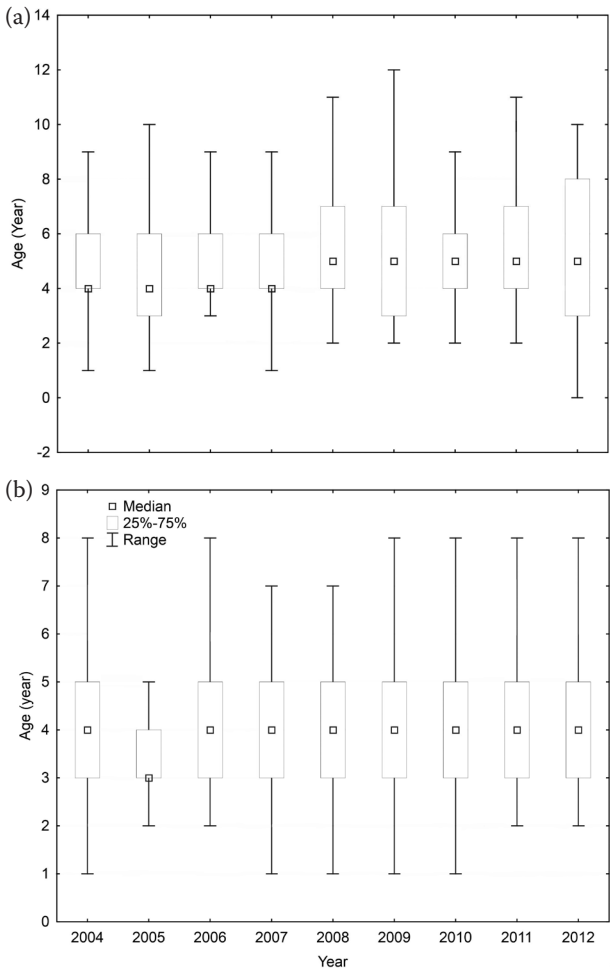

Fig. 6. The median of age of harvested red deer (a) and sika deer (b) individuals during the last decades (2004–2014)

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