

Genetic relationships within colonies suggest genetic monogamy in the Eurasian beaver (*Castor fiber*)

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Abstract Social monogamy, considered rare in mammals, has been described in two species of beaver, the Eurasian beaver (*Castor fiber*), and the North American beaver (*Castor canadensis*). Social monogamy, however, does not necessarily imply genetic monogamy. For example, in group living mammals, females may engage in extra-pair copulations as a result of increased female mate choice opportunities. Recently, following genetic analysis, a wide range of genetic relationships among colony members have been documented in the North American beaver, including extra-pair paternity. Here, we used microsatellite loci to provide parentage estimates from colonies of the Eurasian beaver in the Kirov region, Russia. No evidence for the presence of any extra-pair young was detected. However, in two cases, we found a pair of unrelated males inhabiting a single colony. Our results sug-

gest that while colonies may comprise both related and unrelated individuals, the genetic mating system appears to match that of the previously inferred social monogamy.

Keywords Extra-pair paternity · Family group · Mating system · Spatial structure · Pairwise relatedness

Introduction

The availability of genetic tools for paternity assignment has initiated renewed interest in mammalian mating systems including social monogamy which is considered an infrequent system among mammals (Kleiman 1977; Lukas and Clutton-Brock 2012). Because pair-living animals may engage in copulations outside the pair, social monogamy is not necessarily associated with genetic monogamy. Strict genetic monogamy appears to be extremely rare in mammals. It has been hitherto reliably reported for only five mammalian species *Peromyscus californicus* Ribble 1991, *Madoqua kirkii* Brotherton et al. 1997, *Hypogeomys antimena* Sommer and Tichy 1999, *Canis latrans* Hennessy et al. 2012, and *Aotus azarae* Huck et al. 2014.

In general, social structure seems to affect the rates of extra-pair paternity in socially monogamous mammals (Jennions and Petrie 2000; Cohas and Allainé 2009). Living in families offers higher opportunity for female choice due to the presence of potential mates both within and outside the family, and also limits the efficiency of male mate guarding (Lardy et al. 2012). On the other hand, high level of kinship between family group members may lower the rates of extra-pair paternity owing to reproductive altruism (Lukas and Clutton-Brock 2012) or reduced potential for “good gene” advantage of female promiscuity (Petrie and Lipsitch 1994).

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It has been proposed that beavers, in which social and genetic monogamy has been traditionally assumed, live in singular breeding social groups, i.e., groups where only one pair is responsible for all breeding (Hayes 2000), called colonies (see Baker and Hill 2003 for discussion of the appropriateness of the term colony in beavers). Hence, beavers are optimal model species for studying the effect of living in family groups on extra-pair paternity. Although North American beaver (*C. canadensis*) and Eurasian beaver (*C. fiber*) diverged from a common ancestor as early as 7 mya (Horn et al. 2011), they share many ecological and behavioural characteristics (Müller-Schwarze 2011). Beavers live in small groups comprising mostly a single adult pair with offspring, frequently accompanied by reproductively inactive subadults, i.e., young that were (assumably) born to the same parents in previous years (Baker and Hill 2003; Müller-Schwarze 2011). However, communal denning of two or even three females has also been reported in the North America beaver (Wheatley 1993; Fischer et al. 2010) but is unknown in the Eurasian beaver. Correspondingly, repeated attempts to establish artificial breeding groups containing more than one adult female failed in the Eurasian beaver (Lavrov 1989). Beavers express typical traits of monogamous mammals (sensu Kleiman 1977): duration of the breeding period and female oestrus is short (Wilsson 1971; Sun 2003; Baker and Hill 2003; Müller-Schwarze 2011), sexual dimorphism is largely reduced both in morphology and behaviour (Herr and Rosell 2004), adult males provide substantial parental care, adults live in stable pairs, desertion of a mate is rare and occurs solely after the death of one of the pair, sexual maturation is delayed, and older offspring help in rearing young (Hinze 1960; Wilsson 1971; Patenaude 1983; Baker and Hill 2003; Müller-Schwarze 2011). Relatively small testes mass and highly divergent sperm morphology compared to other rodents suggest low levels of sperm competition (Kenagy and Trombulak 1986; Bierla et al. 2007; Soulsbury 2010). Both sexes engage in territory marking using the contents of castor sacs and secretions of the anal glands (Wilsson 1971; Svendsen 1980); however, males were shown to invest more in scent marks in summer during female lactation (Rosell and Thomsen 2006). The scent marks serve as a tool of neighbor–stranger discrimination (Rosell and Bjørkøyli 2002) and dominance assessment (Rosell et al. 2000; Tinnesand et al. 2013).

The view of obligate genetic monogamy and first-order relationship of beaver colony members has recently been challenged in the North America beaver. Microsatellite analysis revealed that unrelated individuals occur in beaver colonies and more than 50 % of litters were sired by more than one male (Crawford et al. 2008b). However, observations from captivity suggest that the North American beaver and the Eurasian beaver differ in the pattern of association between mating partners. Lavrov (1989) reports difficulties in establishing breeding pairs of the Eurasian beaver in enclosures

which sharply contrasts with ease of artificial pair formation in the North American beaver. Given that the close association between pair partners has been suggested to be linked with the evolution of genetic monogamy in mammals (Clutton-Brock and Isvaran 2006; Huck et al. 2014), we hypothesized that the beaver species differ in their genetic mating system. Genetic studies of the Eurasian beaver family structure are missing to our knowledge. Hence, the aim of the present study was to examine paternity and genetic relationships between adult individuals within Eurasian beaver colonies using genetic methods.

Material and methods

Sampling

Samples were obtained in the Kotelnich district of the Kirov region, Russia (Fig. 1), from June 3rd to July 3rd 2012. Beavers in the Kirov region originated from multiple reintroductions from Voronezh and Belarus relict populations in the 20th century (Saveljev 2001; Milishnikov and Saveljev 2001; Saveljev and Milishnikov 2002). Population size reached 40,000 individuals in 2012 (1 beaver per 3-km² density). Beavers in the Kotelnich district are exposed to natural predators, e.g., wolf, and had been trapped by man until 2010 when beaver hunting was abandoned in the region.

Fifteen active beaver colonies (Table 1) were found at tributaries of the Moloma River during extensive search in an area of approximately 450 km². Each colony comprised a system of dams (up to 7), and burrows and/or lodges stretching up to 800-m length along a river. Water level in every dam was lowered, and beavers were driven out of a burrow or a lodge by specially trained dogs and were trapped into landing nets. Trapped individuals were transported into a field laboratory where a small biopsy sample of foot webbing was obtained and stored in pure ethanol. Sex and age of individuals were identified using a combination of morphological traits (see Stubbe et al. 2003 for details). The mating season in the Kirov region takes part in February and March, and the gestation period is 107 days on average (Lavrov 1960). Hence, kits (young of the current year) were presumably at the age of roughly 1 month during the trapping, which is in agreement with their body mass (from 1 to 1.5 kg).

Genetic analysis

Samples were dried, and DNA was extracted using the DNeasy Blood and Tissue kit (Qiagen). Individuals were genotyped at 26 microsatellite loci designed for beavers (Crawford et al. 2008a; Pelz-Serrano et al. 2009; Frosch et al. 2011) following the original protocols. We redesigned seven primers using flanking sequences deposited in the

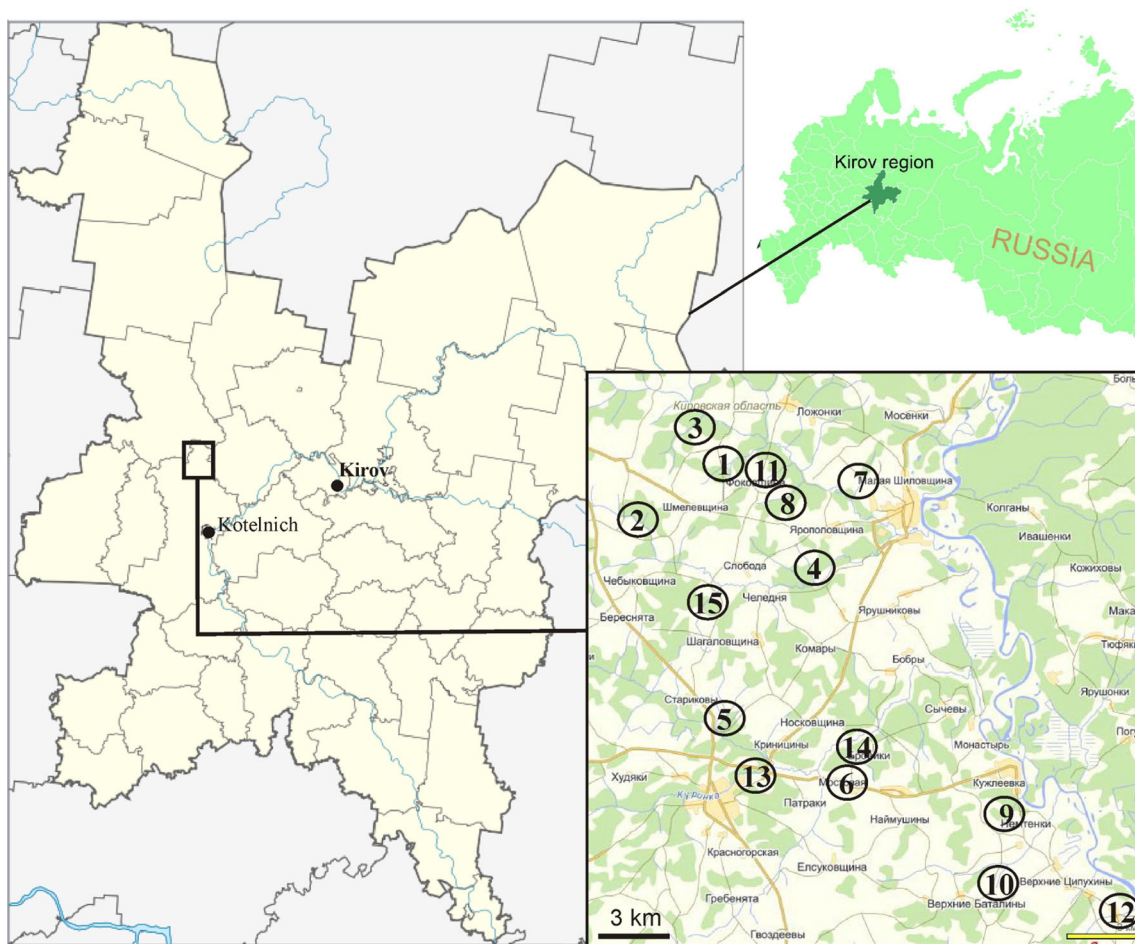


Fig. 1 Study area and location of beaver colonies

GenBank (Table 2), because amplification of several loci using primers originally designed for the North American beaver had poor efficiency in the Eurasian beaver. PCR products were analyzed using ABI PRISM® 3100 Genetic Analyzer (Applied Biosystems). Genotypes were scored with the GeneMarker® version 1.9 software (Softgenetics). Locus characteristics were calculated in Cervus3.0.3 (Field Genetics Ltd, Marshall et al. 1998; Kalinowski et al. 2007). Eight monomorphic loci (Cca5, Cca20, CF5, CF7, CF21, CF30, CF48, and CF49) were not used for further analyses. Presence of null alleles (alleles that fail to amplify) can introduce bias in paternity studies (Dakin and Avise 2004). Given the fact that deviation from Hardy–Weinberg equilibrium suggests presence of null alleles or other genotyping errors, we excluded three loci (Cca112, CF18, and CF33) that showed significant heterozygote deficit. We used MICRO-CHECKER (van Oosterhout et al. 2004) to estimate frequency of genotyping errors (null alleles, large allele dropouts, and stuttering) in the final set of 15 unexcluded loci. No loci showed evidence for genotyping errors, and the analysis suggested that the population was in Hardy–Weinberg equilibrium.

Given the fact that beavers are characterized by long pair bond, we assumed that the adults accompanying subadults were also their social parents. Hence, both kits and subadults were used for the paternity analysis as young. We used a combination of exclusion, categorical allocation, and sibship reconstruction (Jones et al. 2010) for parentage analysis. First, we used Cervus3.0.3 to find allelic mismatches between young and adults and to identify the most likely parents. The categorical allocation in Cervus was based on simulations of 100,000 young. We found no mismatches between young and putative mothers (females inhabiting the same colony as young), and the putative mothers were always indicated as the most likely parent in Cervus (at 95 % confidence in five comparisons and 80 % in the remaining five). Hence, we assumed that the putative mothers are also genetic mothers of young and used this information for further calculations of paternity.

We performed several independent runs of Colony 2.0.4.5 (Jones and Wang 2010) to assess multiple paternity in families for which the putative father was not sampled. Colony estimates the sibship among offspring and finds the most likely

Table 1 Composition of beaver colonies

Colony no. (same as on Fig. 1)	Adult F	Adult M	Subadult (unknown sex)	Subadult M	Subadult F	Juvenile
<i>Colonies with offspring</i>						
1		1		2	2	
2	1	1		1	1	1
5	1	1				1(2)
6		1		1	1	
7	1					3(1)
10	1	2				1(1)
12	1					2
13		1				1
15		(1)	(1)			1(3)
<i>Colonies without offspring</i>						
3	1	1				
4		1				
8		2				
9		1				
11	1	1				
14	(1)	(1)				

Individuals that were observed in colonies but escaped before sampling are given in brackets
M male, *F* female

clusters of half- and full-siblings. However, given that adequate estimates are expected predominantly for larger litters, the program use has obvious limitations in families containing one or two young, a frequent situation found in beavers. Colony finds the most likely solution; however, its capability to provide statistical significance of the results is limited. Hence, hypothesis concerning the relationship between pairs of

individuals was further tested in Kingroup v2_090501 (Konovalov et al. 2004). Kingroup implements a maximum likelihood approach to pedigree relationship and estimates likelihood for alternative relationship hypotheses.

We used SPAGeDi version 1.4 (Hardy and Vekemans 2002) to analyze spatial genetic structure at the individual level. SPAGeDi estimates relatedness coefficients between

Table 2 Microsatellite loci used for genetic analyses

Locus	k	Size range	H _O	H _E	New forward (F:) or reverse (R:) primer sequence
CF6	2	134–136	0.395	0.506	
CF17	2	206–221	0.421	0.417	
CF19	4	187–190	0.605	0.673	F: CAGGAGATGGAGACAAAAGGAT R: GCCATACGTAGTCCCCTTTG
CF31	3	218–225	0.316	0.279	
CF32	4	151–159	0.605	0.612	
CF44	5	204–215	0.737	0.735	
Cca4	3	378–392	0.342	0.330	
Cca8	3	380–404	0.605	0.650	
Cca13	3	264–268	0.079	0.078	
Cca18	2	219–221	0.289	0.287	
Cca19	4	276–285	0.649	0.645	
Cca56	2	212–216	0.263	0.269	R: CAAGAGTCCAGTGTGTGCTG
Cca62	3	232–242	0.649	0.605	F: CCAAGTGAATTAACATACCCATCA R: GAAAATCCCGGAGAATGGAT
Cca76	2	196 - 198	0.242	0.302	R: CCATGCTATGTGGCATT TTT
Cca92	2	196 - 198	0.263	0.305	R: ACTGTGGAAGCTCTGGGAGT

Locus characteristics are based on genotypes of 38 beavers. Number of alleles (k), allele size range, observed (H_O) and expected (H_E) heterozygosity, and redesigned primers are given

individuals to characterize association between genetic and spatial distances. The program allows to treat individuals from a same location as dependent, and thus, it does not include pairwise comparisons of individuals from a same colony into analyses. Pairwise relatedness was calculated according to Queller and Goodnight (1989). Significance of associations was tested using 10,000 permutations. Jackknifing over loci was used to calculate multilocus relatedness statistics.

Results

Marker variability

Thirty-eight beavers were genotyped at 15 polymorphic loci. Two to five (average 2.9) alleles were observed across loci (Table 2). Combined nonexclusion probability for the second parent was 0.015, which suggests that the set is suitable for paternity analysis (Marshall et al. 1998).

Spatial relatedness and colony composition

Pairwise distance between colonies ranged from 1.6 to 27.1 km. No relationship between pairwise relatedness and distance between colonies was found (all samples: $n=658$ pairs, $r^2=4\times 10^{-8}$, $p=0.94$; adult males: $n=78$ pairs, $r^2=7\times 10^{-8}$, $p=0.95$; adult females: $n=21$ pairs, $r^2=0.043$, $p=0.30$). Estimates of pairwise relatedness (R) among adults were close to zero (males: -0.084 ± 0.001 SE; females -0.168 ± 0.002 SE).

In nine of the 15 colonies, families with between one and five (average 2.9) young (juveniles or subadults) were found (Table 1). Young were accompanied with a varying number of adults (Table 1). Six colonies contained only adults. Among the 15 colonies mentioned above, two were composed solely of 2 adult males each. The pair of males was always captured in a close distance in the same pond. While in one colony, the males were of similar weight (18.6 and 18.0 kg), there was a large weight difference among males in the second one (16.4 and 22.6 kg). The males from a pair inhabiting a single colony did not share any allele at three and five loci (respectively, for the two colonies). In both colonies, Kingroup analysis revealed that males were unrelated ($p<0.05$), as opposed to the alternative scenarios of parent–offspring, full-sib, or half-sibling relationships.

Paternity analysis

In four families (2, 5, 6, 13) containing a single adult male, the putative father, i.e., the male sharing the colony with young, was also indicated as the most likely genetic father for young in his colony. In family 10, one of the two males concurrently present in the colony was excluded due to mismatches at four loci while the second male did not show any mismatch with

young and was the most likely candidate in Cervus (genetic father at 80 % confidence). Four subadults shared the colony 1 with an adult male (their putative father) while an adult female was missing. The putative father differed from the subadults by up to 2 mismatches (0, 0, 1, and 2 mismatches) and was not indicated as the most likely genetic parent in Cervus. A male from the neighboring colony 3 was suggested as the most likely (but not significantly exclusive, <80 % confidence) parent for two of the subadults in Cervus, and the male was also the only male in our sample that had zero mismatches with all the four subadults. For young in three families (7, 12, and 15), where the putative father was absent or unsampled, Cervus did not suggest any genetic father from the sampled males at a sufficient level (>80 %) of significance.

Relationship among young

Three families (1, 2, and 7) had three or more sampled young which allowed detailed analysis of their relationship. In all three families, the full-sib relationship among offspring was the best Colony maximum likelihood estimate which was further corroborated in Kingroup where the hypothesis of full-sibship was significantly better than half-sibship or unrelatedness ($p<0.05$). In families with two young, Colony suggested half-sibling relationship (families 6 and 12). However, Kingroup revealed that the hypothesis of half-sibship was not significantly better than full-sibship. We suggest that the uncertainty of sibship may be attributed to insufficient sample size (only two young in families) and low number of alleles at the used loci (Table 2). It should be noted that the full-sibling relationship among young in family 6 was previously suggested in the Cervus analysis.

Discussion

Our genetic analyses suggest that the Eurasian beaver and the North American beaver differ in genetic mating system. While Crawford et al. (2008b) found that more than half of the litters (5 of 9 litters) of the North American beaver contained young sired by more than one male, we have not found any clear support for the presence of extra-pair paternity in our sample of 18 young from 9 colonies. However, in one colony, where an adult female was missing, the subadults did not match the putative father. Nevertheless, the offspring were full sibships, and hence, we speculate that after death or desertion of the adult female, the genetic father of young abandoned the family and set up the new neighboring colony 3 with a new female, while a new male joined the subadults in colony 1 to find mates. Even though our interpretation seems likely, it should be noted that in this particular case, we cannot fully exclude alternative hypotheses involving extra-pair fertility. However, the close relationship of young suggests that they

were conceived by the same father regardless whether it was the social parent of young or a male engaging in extra-pair copulations.

On the other hand, the mating systems are often flexible (Lott 1984), and beavers appear to adapt their reproductive strategies according to local environmental or social conditions. The frequency of extra-pair paternity can be influenced by population density (Lott 1984; Bryja et al. 2008) and in beavers also by family size. While a smaller population density would lower the probability of finding extra-pair mate, the lower litter size would decrease our chance of extra-pair young detection especially when the genotype of the putative father is missing. The density of beaver colonies was indeed higher at the two Illinois localities (one colony/2.5 km of stream and one colony/0.3 km², respectively) where paternity was examined in the North American beaver (Crawford et al. 2008b). The density of beaver colonies examined in this study was approximately one colony/2.5 km² (one colony/4 km of stream). The beaver families in the present study were also smaller. While Crawford et al. (2008b) reported a mean of 3.8 and 9.0, respectively, for the two investigated regions, mean colony size was 3.3 in this study.

Mating patterns can be also influenced by genetic variability. In birds, it has been evidenced that low genetic diversity leads to relaxed selection on extra-pair paternity (Petrie et al. 1998; Møller et al. 2008; Gohli et al. 2013). Thus, if this applies also to beaver, it might be hypothesized that more females could be engaged in seeking extra-pair mates to improve genetic quality of offspring when males are more variable in their genetic quality. Hence, lower rates of extra-pair paternity can be expected in the Eurasian beaver in which genetic variability was substantially reduced due to overhunting (Ellegren et al. 1993; Babik et al. 2005; Ducroz et al. 2005; Durka et al. 2005). Moreover, a female seeking for extra-pair copulations faces the risk of loss of paternal care provided by her social partner. Paternal care is extensive in beaver and can influence young survival in winter when they are fully dependent on food reserves collected by the whole family (Wilsson 1971; Patenaude 1983; Müller-Schwarze 2011). Hence, it is possible that due to little genetic variation among the Eurasian beaver males, the “good gene” advantage of female extra-pair mating is not large enough to outweigh the risk of paternal care loss. However, it should be noted that genetic variability was partially restored in beavers in the Kirov region due to repeated introductions from various sources (Milishnikov and Saveljev 2001; Saveljev and Milishnikov 2002). Moreover, it can be argued that the North American beaver also experienced long period of extensive harvesting (Müller-Schwarze 2011). Unfortunately, precise comparison of genetic variability of the two beaver species is not available. However, Pelz-Serrano et al. (2009) reported smaller number of alleles at microsatellite loci in the Eurasian beaver than in the North American beaver.

Genetic monogamy has been traditionally assumed in beavers on the basis of indirect evidence, e.g., expression of typical traits of monogamous mammals or ecological constraints. Beavers have to spend considerable time foraging because they feed on a diet of low nutritional value. Moreover, the building of dams, lodges, and burrows requires large energy investments. Hence, Sun (2003) suggested that energy and time constraints prevent beaver males from leaving their colonies to seek extra-pair copulations. Moving outside the colony also increases the risk of predation or aggressive attack by individuals defending other beaver territories. Nevertheless, inter-colony movements were reported at high population density in the North American beaver (Busher et al. 1983). In the Eurasian beaver, Campbell et al. (2005) observed occasional incursions into adjacent territories at up to 1.5-km distance, and during floods, the beaver territory boundaries can even erode and home ranges overlap (Nitsche 2001). It should also be noted that movements of beavers in the Kirov region are restricted during the mating season by extensive snow cover and low temperatures. Beavers during winter are active almost exclusively under ice or snow (Safonov 1965, 1971). While tunnels under snow reach only up to 15-m distance, indirect evidence of contacts of individuals from different colonies suggests that beavers can occasionally cover the distance between separate colonies under ice (Safonov 1965).

In this study, we found in two cases a pair of unrelated males in a single pond which suggests that unrelated individuals can occasionally enter beaver family quarters. Similar frequencies of possible incursions were found in the North American beaver (Crawford et al. 2008b). Neither the design of our study nor the analyses of Crawford et al. (2008b) allow an examination whether the unrelated individuals are accepted in colonies for longer time periods or whether the visits are just transient. Observations in captivity showed strong territoriality and low tolerance to same-sex adults both in males and females in the Eurasian beaver (Lavrov 1989). However, there is anecdotal evidence from a German wildlife rescue station that presumably unrelated individuals of the same sex can sometimes tolerate each other and live in a single enclosure (C. Frosch, personal communication). We speculate that the high energy demands of dam building and food storing may cause tolerance to newcomers to form cooperative coalitions including unrelated individuals as has been observed, e.g., in lions (Packer and Pusey 1982). However, the disentangling of tolerance toward unrelated individuals in beavers requires well-designed long-term studies. It should be also noted that beaver tolerance for newcomers may differ in summer, when our sampling was conducted, from the situation in February and March when Kirov region beavers copulate. We cannot exclude the possibility that males engage more in mate guarding and territoriality when females come into oestrus.

Dispersal distance and age at dispersal vary considerably in the European beaver (Hartman 1997). Mark-recapture

experiments at the Azas River (Tuva, Russia) showed shifts of subadults at considerable distances (from 0 to 85 km, 17 km on average) within 2 years (Saveljev et al. 2010). In accordance, our observations of low average pairwise relatedness of adults and the absence of association between genetic and spatial distances suggest that gene flow is intense enough to prevent formation of a local spatial genetic structure.

In conclusion, we have not found any clear evidence for extra-pair paternity in our sample of the Eurasian beaver families. This suggests that Eurasian beaver ranks among the few genetically monogamous mammalian species. However, our sampling is rather limited, and studies of other populations based on larger number of individuals are needed to corroborate our findings. Unfortunately, such studies are technically challenging. The set of microsatellite loci was usable for paternity analysis of beaver families in the Kirov region which implies that the same set can be used in the genetically diverse admixed populations in Western Europe (Frosch et al. 2014; Senn et al. 2014). However, it should be noted that the number of alleles was small for every locus and almost one third of loci were even monomorphic. Beavers in the Kirov region originated from reintroductions from various sources and hence express higher level of genetic diversity than relict beaver populations (Senn et al. 2014). Hence, paternity analysis using microsatellites would be more complicated or even impossible in relict populations of beaver, where genetic diversity is particularly low (Ellegren et al. 1993; Babik et al. 2005; Ducroz et al. 2005; Durka et al. 2005; Senn et al. 2014). However, a recently developed large set of SNP loci (Senn et al. 2013) would likely overcome the limitations of paternity analysis in beaver relict populations.

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Ethical standards Research followed Russian federal hunting law (2009 N 209).

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