

Almost faithful: SNP markers reveal low levels of extra-pair paternity in the Eurasian beavers

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Mating systems largely affect individual reproductive strategies which further drives evolution. Monogamy, where males and females form exclusive pairs for more than one breeding season, is particularly intriguing in this context, as there are real and potential costs of genetic monogamy to both sexes. However, molecular studies in a variety of species have revealed that social monogamy does not necessarily imply genetic monogamy due to occurrence of extra-pair copulations resulting in extra-pair offspring. Although common in birds, <10% of mammals are monogamous. Here we use single nucleotide polymorphism (SNP) to investigate the genetic mating system of the Eurasian beaver (*Castor fiber*), a species traditionally considered to be not only socially but also genetically monogamous. We found evidence for low frequency of extra-pair paternity (EPP) and multiple paternity within litter. Only 5.4% young were produced by EPP and only 7% of litter contain at least one extra-pair young. Moreover, we found indications that only pairings of old individuals engaged in EPP. None of these pairs produced more than one litter as a result of EPP and none of the EPP events resulted in mate change. Our findings suggest that EPP in beavers might be the consequence of a lapse in mate guarding ability of old males.

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Abstract

Mating systems largely affect individual reproductive strategies which further drives evolution. Monogamy, where males and females form exclusive pairs for more than one breeding season, is particularly intriguing in this context, as there are real and potential costs of genetic monogamy to both sexes. However, molecular studies in a variety of species have revealed that social monogamy does not necessarily imply genetic monogamy due to occurrence of extra-pair copulations resulting in extra-pair offspring. Although common in birds, <10% of mammals are

monogamous. Here we use single nucleotide polymorphism (SNP) to investigate the genetic mating system of the Eurasian beaver (*Castor fiber*), a species traditionally considered to be not only socially but also genetically monogamous. We found evidence for low frequency of extra-pair paternity (EPP) and multiple paternity within litter. Only 5.4% young were produced by EPP and only 7% of litter contain at least one extra-pair young. Moreover, we found indications that only pairings of old individuals engaged in EPP. None of these pairs produced more than one litter as a result of EPP and none of the EPP events resulted in mate change. Our findings suggest that EPP in beavers might be the consequence of a lapse in mate guarding ability of old males.

Introduction

Understanding mating systems is essential as they reflect individual reproductive strategies to maximize reproductive success and thus drive evolution (Smith 1978). Social monogamy, where males and females form exclusive pairs for at-least one breeding seasons or even life (Lukas and Clutton-Brock 2013), is particularly intriguing in this context (Dobson et al. 2010). Especially in mammals, this reproductive strategy evolved in species for which intra-sexual competition among females is intense and breeding females are intolerant of each other (Lukas and Clutton-Brock 2013). Under these circumstances, guarding individual females could be the most successful breeding strategy for males, as they cannot defend access to several females (Emlen and Oring 1977, Busher et al. 2007, Fukuda et al. 2017). Although male mate guarding ensures male reproductive success by monopolizing their female, it constrains males into monogamy (Schubert et al. 2009). Therefore, Brotherton and Komers (2003) suggest that male mate guarding can also explain the evolution of monogamy. The costs of genetic monogamy for both sexes, however, are clear: males renounce the opportunity to increase their reproductive success by mating with multiple females (Krebs and Davies 2009), whereas females give up genetic variation among offspring (Jennions and Petrie 2000). To offset the costs of monogamy, both sexes could engage in extra-pair copulations (EPC) leading to extra-pair paternity (EPP). Males would thereby enhance their reproductive success without increasing paternal investment (Trivers 1972, Zhao et al. 2016) and eventually increase potential for sexual selection (Vedder et al. 2011). Females would obtain primarily genetic benefits (Jennions and Petrie 2000, Foerster et al. 2003), such as increased fitness of their offspring (e.g. Kempenaers et al. 1992, Westneat and Stewart 2003, Bonderud et al. 2018), or increased overall genetic diversity of their young (Tregenza and Wedell 2000, Cohas et al. 2007). EPP may also result in higher probability of conception (Uller and Olsson 2005), bigger litter size (Hoogland 2013) and increased inclusive fitness for females (Bowers et al. 2015).

Age plays an important role in the occurrence of EPC. In some species, EPC declines with female age, for example in the European Pied Flycatcher (*Ficedula hypoleuca*) (Moreno et al. 2015). In comparison, EPC increases with age in passerines, where older males are more successful at EPC (Tarof et al. 2011, Cleasby and Nakagawa 2012). Social partners' age also affects EPC occurrence for example in House wrens, (*Troglodytes aedon*) females engage more in EPC as the age of social male increases (Bowers et al. 2015).

Studies using molecular techniques have revealed that social monogamy does indeed not necessarily imply genetic monogamy: while 90% of bird species are socially monogamous (Cockburn 2006), out of these, less than 25% are also genetically monogamous (reviewed in Griffith et al. 2002, Bojarska et al. 2018). In comparison, monogamy in mammals is less common and only 3-9% of the species are defined as socially monogamous (Trivers 1972, Lukas and Clutton-Brock 2013). However, genetic studies with adequate sample sizes that rule out genetic promiscuity are scarce amongst mammals (Huck et al. 2014). The proportion of EPP in natural populations of socially monogamous mammals varies considerably from zero in e.g. Kirk's dik-dik (*Madoqua kirkii*, (Brotherton et al. 1997) and Azara's owl monkeys (*Aotus azarae*), to 0.52 in the swift fox (*Vulpes velox*) (Kitchen et al. 2006) and 0.87 in North American beavers (*Castor canadensis*) (Crawford et al. 2008). This suggests that – contrary to previous viewpoints (e.g. Clutton-Brock and Isvaran 2006, Cohas and Allainé 2009) - strict genetic monogamy might be rare in socially monogamous mammals, mirroring results in birds (Griffith et al. 2002). Eurasian (*Castor fiber*) and North American beavers are among the few non-primate mammals displaying social monogamy (Svendsen 1989, Sun et al. 2003). Busher et al. (2007) reviewed several studies in beavers, testing hypotheses on male parental care, high costs of polygyny, and on female aggression to understand the evolution of monogamy in this species. Based on these studies they suggest that “...the beaver mating system represents an ideal model to investigate the evolution of monogamy” (Busher et al. 2007). Although previous studies show that the closely related North American beaver frequently engages in extra-pair mating with 56% of litters containing extra-pair young (Crawford et al. 2008), a similar study in Eurasian beavers in Kirov, Russia found no evidence of EPP (Syrůčková et al. 2015). This study, however, was based on a very low sample size of kits (n= 10). Since the Eurasian beaver population in Russia was at a much lower density compared to Crawford et al.'s (2008) study, Syrůčková et al. (2015) hypothesized that density could explain the absence of evidence of EPP in European beavers. Here, we used 19 years of parentage data from one of the most extensive long-term individual-based studies on Eurasian beavers in the world (Steyaert et al. 2015). The population in our study area is at carrying capacity (Campbell et al. 2005, Steyaert et al. 2015), allowing us the opportunity to investigate the mating system of Eurasian beavers at high density. Our aims were i) to investigate the genetic mating system of the Eurasian beaver to elucidate the occurrence of EPP; and ii) to assess the effects of parental age on potential occurrence of EPP. We discuss our results in view of understanding the cost and benefits of mammalian monogamy and EPP.

Materials & Methods

Study species

Eurasian beavers are large (>20kg: Wilsson 1971, Müller-Schwarze and Sun 2003), semi-aquatic, sexually monomorphic rodents with a lifespan of up-to 20 years (Wilsson 1971, Campbell et al. 2005). They typically form reproductive pairs shortly after dispersal from their

natal territory (Mayer et al. 2017d), and show strong site fidelity until a mate is displaced by a same-sex competitor or dies (Svendsen 1989, Müller-Schwarze and Sun 2003, but see Crawford et al. 2008). Copulations occur in late January - February during a short period of female estrus (12-24 hours; Doboszynska and Zurowski 1983), and females give birth to a single litter, comprising 2-5 offspring (termed “kits”) in May – June (Wilsson 1971, Parker et al. 2017). Both partners contribute to parental care, and kits first emerge from the communal den (“lodge”) when fully weaned, six to eight weeks later (Wilsson 1971). Sexual maturity is attained at age 1.5 – 2.5 years (Wilsson 1971, Parker et al. 2017), whereupon offspring, of either sex, disperse if territory vacancies are available (Hartman 1997, Mayer et al. 2017b). Although only the dominant pair breeds (Svendsen 1989, Mayer et al. 2017b), extended family groups can form due to retention of kits from the current and/or previous breeding seasons (Wilsson 1971, Svendsen 1989). Because there is never more than one dominant breeding pair in a family group, any offspring remaining in the natal territory after attaining sexual maturity are termed subordinates. In most cases, all subordinates are siblings that do not reproduce until they acquire dominant status either by dispersal or by taking over their natal territory after the death of their parents. Occasionally, dispersing individuals are also caught in the same territory. Since there is no evidence of helper function by subordinates, beavers cannot be classed as co-operative breeders. Groups defend and scent-mark their shared territory (Rosell et al. 1998, Müller-Schwarze and Sun 2003), and territorial borders typically remain stable over generations (Steyaert et al. 2015). Territories of neighboring beaver families are non-overlapping (Herr and Rosell 2004), and intruding conspecifics are chased aggressively (Svendsen 1989, Nolet and Rosell 1994).

Study area and data collection

We analyzed the DNA from hair samples of 424 individuals caught between March 1998 and October 2016 as part of an ongoing long-term beaver population study (Campbell et al. 2012, Campbell et al. 2013) along the rivers Straumen, Gvarv and Saua in Telemark County, southern Norway. These rivers form part of the catchment of Lake Norsjø, and contain lakes along parts of their length, resulting in limited fluctuations in water temperature and reduced ice cover in winter (Campbell RD 2010). The population is considered saturated as territories border each other directly (Campbell et al. 2005). The study area comprises ca. 25 territories (Mayer et al. 2017d) and average annual population densities varied between 2.7 and 7 individuals per group (mean \pm SD: 4.3 ± 0.9) between 1998 – 2015 with the average of 0.35 colonies/square km (Mayer et al. 2017d). Beavers were captured with landing nets from a motorboat, immobilized through manual restraint in cloth sacks while measurements were taken and samples collected, and animals were typically released after 15-20 min (Rosell and Hovde 2001). All individuals were assigned to an age-class (0 years = kit, 1 years of age = yearling, 2 years = subadults, ≥ 3 years = adult) based on previous capture history or body-weight (Rosell et al. 2010, Campbell et al. 2013). Beavers (age >2 years) that were captured only for one or two breeding seasons and not observed thereafter, were termed floaters. All new captures were tagged with a microchip (Avid or Trovan), and marked with unique color-plastic (Dalton) and metal (National Band and

Tag Co.) ear-tag combinations (Campbell et al. 2012). Beavers were sexed on the basis of the color of their anal gland secretion (AGS; Rosell and Sun 1999). Dominance was determined through multiple recapture events of adults in the same territory in absence of the previous dominant same-sex individual, and, in females, through signs of lactation (Campbell et al. 2012). Territories were surveyed 30 ± 15 SD nights annually (Campbell et al. 2012). Additional long-term data include information about territory borders, family composition, family member replacements, length of pair bonds, as well as breeding and dispersal events reaching back to 1998. All capturing and handling procedures were approved by the Norwegian Experimental Animal Research Board (FOTS id 742, id 2170, 2579, 4384, 6282, 8687) and the Norwegian Directorate for Nature Management (2008/14367 ART-VI-ID, archive code 444.5, 446.15/3, 14415) which also granted us permission to conduct fieldwork in our study area.

Genetic analyses

Genetic samples were collected from all individuals by plucking 20-40 guard hairs with follicles (presence determined by visual inspection) from the lower back. Hair samples were stored in paper envelopes at room temperature. DNA was extracted using QIAGEN® blood and tissue kits (Cat. No. 69506) with the following modifications to the standard kit protocols: 5 µl dithiothreitol (DTT) was added while incubating samples at 56°C for complete hair strand degradation followed by 200 µl ATL Buffer instead of 180 µl. The DNA was then eluted in 100 µl AE buffer, and DNA purity and concentration were checked by Picodrop Microlitre Spectrophotometer version 3.1 (Picodrop Ltd). All samples were diluted to a final concentration of 5ng/ µl for further analysis.

From a panel of 2,579 high confidence polymorphic SNPs discovered within the Eurasian beaver (Senn et al. 2013), 306 were genotyped in populations across Eurasia (Senn et al. 2014). From those 306 SNPs, we selected 30 SNPs with the highest joint ranking for Probability of Identity (PID) in Norwegian and Bavarian (Germany) beaver population samples genotyped in Senn et al. (2014). SNP genotyping in this study was performed using a StepOne™ Real-Time (Applied Biosystems) PCR instrument, where 2 µl (5ng/µl) DNA was added to 10 µl PCR mixture containing 5 µl of TaqMan™ GTXpress™ along with 900nM of both primer concentration and 250nM of TaqMan® probes using proprietary fluorescent TaqMan® oligonucleotide probes labelled with VIC and FAM reporter dyes. The thermal profile for real-time PCR was as follows: initial denaturation at 95°C for 20 sec followed by 40 cycles of 95°C for 3 sec and 60°C for 30 sec. No-template control was added to each plate. For calculating the genotyping error rate, 10 % of samples were randomly selected and re-analyzed. The same genotyping error rate was used for parentage analysis.

SNP characteristics

Sufficient DNA quality was obtained from 84 % (356/424) of the samples. Three SNPs (E12, F4 and G9) had a high rate of genotyping error (>5%) and were excluded from further data analysis, thus leaving 27 SNPs. Basic genetic parameters (allele frequencies, expected and observed

heterozygosity), and deviations from the Hardy-Weinberg equilibrium were calculated using CERVUS 3.0.7 (Kalinowski et al. 2007, 2010; Table 1). The number of individuals typed at each locus ranged from 326 – 356 (92 – 100%). No SNPs deviated significantly from Hardy-Weinberg equilibrium. Twenty-four of the 27 SNP markers had an observed heterozygosity index > 0.3 , 17 of 27 > 0.4 , and two of 27 > 0.5 . The average non-exclusion probability for the second parent was 0.008, suggesting that the set of SNPs was suitable for paternity analyses (Marshall et al. 1998).

Parentage analysis

Parentage was analyzed in CERVUS 3.0, which uses a maximum likelihood-based approach (Marshall et al. 1998, Kalinowski et al. 2007), which is more effective at accommodating error rates than other methods, such as exclusion analysis (Marshall et al. 1998). CERVUS uses simulations of allele frequencies of candidate parents to calculate the natural logarithm of likelihood ratio (LOD score). CERVUS then assigns paternity/ maternity based on the difference between LOD scores of the most likely father/ mother and all other candidate fathers/ mothers at user defined confidence. We used 95% as conservative confidence interval and 80% as relaxed confidence as well as 5% genotyping error rate for both paternity and maternity analysis. We used 90% cut off for candidate fathers and candidate mothers sampled.

Complementary long-term data were used to create candidate father, candidate mother and candidate offspring files. We restricted parentage analysis to beaver families where both putative parents were genotyped successfully and offspring were captured for the first time as kits or yearlings, because older individuals are likely to be dispersers (i.e. offspring from non-resident parents; Hartman 1997, Mayer et al. 2017b). First, we used CERVUS to determine maternity for each young by including the dominant female in the kit's assumed natal territory, as well as the breeding females from each neighboring territory to control for observation errors. We then tested if the social partner of the assigned mother was also the genetic father of the young. In these paternity analyses, we included all sexually mature males (including floaters) present within two territories on either side of the kit's natal territory as candidate fathers in order to identify possible extra-pair mates.

Effects of parental age

In order to investigate potential effects of reproductive senescence generally, we correlated the age of mothers and social mates with the number of kits born per year (over the total dataset). Then, to test for any effects of parental age on the occurrence of EPP, we correlated the age of the mother as well as the age of her social mate with the percentage of extra-pair young. We used simple correlations for these analyses, because low EPP sample sizes did not allow for more complex statistical modeling. For all analyses, the level of significance was set to $\alpha < 0.05$. The significance level between $\alpha > 0.05$ and < 0.1 was considered a suggestive trend. All statistical analyses were carried out in SPSS V24.0.0.0 (IBM Corporation).

Ethical statement

All trapping and handling procedures were approved by Norwegian Experimental Animal Board (FOTS id 742, id 2170, 2579, 4384, 6282, 8687) and Norwegian Directorate for Nature Management (2008/14367 ART-VI-ID, archive code 444.5, 446.15/3, 14415), that also granted permission to conduct field work in the research area. All methods were performed according to the relevant guidelines and regulations.

Results

In total, paternity analyses included 166 young from 100 litters born in 48 families for which both candidate parents were genotyped, with 99% of parent pairs assigned at > 80 % probability (i.e., n= 165 kits) and with 83% (i.e., n= 138 kits) assigned at >95% probability (Table 2). In 153 young (92.2%), the mother assigned based on trapping and observational data was confirmed as the genetic mother by CERVUS. In the remaining 13 young (7.8%), the assigned mother was the dominant female in the neighboring family group, indicating mistaken assignment to a family group during capture. The social mate of the assigned mother was confirmed as the genetic father in 157 (94.6%) of the young, and we confirmed EPP in 9 young (5.4 % of young) from seven litters (7 % of litters; Table 2). Two of these offspring had a same-litter sibling fathered by the social mate, providing evidence of multiple paternity within Eurasian beaver litters. In seven extra-pair young, CERVUS assigned the closest neighboring male as the most likely father; in total four different males. Three of these males were the dominant males in the neighboring territory, while one was a nine year old solitary male (fathering three kits in two neighboring territories in 2012) living in a creek between the two territories. We were not able to assign a father with sufficient probability to the remaining two extra-pair young. For one of these young, the neighboring dominant male had never been caught and genotyped, thus excluding him from parentage analysis. In the other unassigned extra-pair young, neither the resident social mate of the assigned mother nor any of the neighboring males were assigned paternity, most likely due to incomplete genotyping of putative parents.

Effects of parental age on EPP

We found a significant positive correlation between the number of extra pair young and the age of the mother (Spearman's rank correlation, $r_s = 0.52$, $N = 12$, $P = 0.04$; Table 3; Figure 2), and the occurrence of EPP also increased with the age of the social male (Spearman's rank correlation, $r_s = 0.46$, $N = 13$, $P = 0.06$; Table 3; Figure 2). In contrast, the number of kits significantly decreased with increasing age of both, the mother (Pearson correlation, $r_p = - 0.66$, $N = 12$, $P = 0.02$; Figure 3) and the father (Pearson correlation, $r_p = - 0.64$, $N = 13$, $P = 0.02$; Figure 3).

In general, the pairs with confirmed EPP consisted of older individuals with average age for males 8.9 ± 4.2 (mean \pm SD; range 3 to 13) and females 9.7 ± 2.5 (range 4 to 15), with overall average age (for both males and females) being 9.2 ± 0.6 . None of the EPP incidences resulted in mate change (i.e. divorce), and all pairs remained together until one of the partners died (in two

of the pairs both partners are still alive two - four years after the occurrence of EPP, and are still together). None of the pairs produced more than one litter with EPP.

Discussion

As compared to previous report (Syrůčková et al. 2015), here we found evidence for EPP as well as for the occurrence of multiple paternity within litters in Eurasian beavers. Our results also suggests that the EPP occurs primarily in the pairs with older individuals at an average age of 9.2 ± 0.6 . At a rate of 0.054 and only 7 (7 %) out of 100 litters, EPP occurred far less frequently in Eurasian beavers than reported for the closely related North American beaver, where rates have been observed to be as high as 0.63 to 0.87 (Crawford et al. 2008) with evidence for EPP in five of nine (56 %) of the investigated litters. Although the low occurrence of EPP in this study limits our ability for complex statistical analysis, it highlights some interesting trends and results; however, they need to be interpreted with caution.

As compared to NA beavers, we found very low levels of EPP in Eurasian beavers (Crawford et al. 2008). These strikingly different levels of EPP are contrary to previous viewpoints that suggested that both species are similar in behavior and biology (Gorbunova et al. 2008, Parker et al. 2012). The North American study area experiences milder winters as compared to our study area, this could increase winter movement of beaver resulting in high rates of EPP. Though, it is plausible that both beaver species might have different mating systems, the simpler explanation could be due to the differences between the design of the study and the data collection methods. For our study, the samples have been collected every year since 1997, with extensive live trapping during autumn and spring. Due to familiarity with the study areas and study population, our observational data had high accuracy as evident by parentage analysis, for which more than 90% of the kits were assigned to the same mother as expected from the observational data. However, for the North American study, the data was collected over a two year period (2005 - 2007; Crawford et al. 2008), by removing all the beavers in a colony over a two week period; which might be a short duration to identify dominant individuals, distinguish between floaters and subordinates, and to establish the territory boundaries. It is likely that a floater can take a residence in the same lodge during that period and happen to be present while trappers were removing all the beavers, resulting in the unreliable finding that unrelated individuals lived in the same colony. Moreover, Crawford et al. (2008) were not able to collect genetic data from all the beavers in the study area that might have also caused the incorrect interpretation of the results. One prerequisite for EPPs is that extra-pair mates are available when the female is receptive. Hence, high population density of sexually mature adults has been proposed as an ecological explanation for the occurrence of EPP in monogamous species, as mate guarding is likely to be more difficult (e.g. Lukas and Clutton-Brock 2013). For instance, in the alpine marmot (*Marmota marmota*), the occurrence of EPCs increased with the number of subordinates present (Cohas et al. 2006). Similarly, the studies of island foxes (*Urocyon littoralis*) (Roemer et al. 2001) and swift foxes (Kitchen et al. 2006) have revealed high rates of EPC in high-density populations. Compared to the Kirov population in Russia (Syrůčková et al. 2015), beaver

population density in our study area is higher (mean colony size 3.3 in Russia, compared to 4.3 in our area) and at carrying capacity (Campbell et al. 2005), possibly explaining why the previous study failed to find evidence for EPP.

Beavers have non-overlapping territories (Herr and Rosell 2004, Campbell et al. 2005, Graf et al. 2016), and territory borders must be crossed to find extra-pair mates, which involves the risk of being detected and attacked by same-sex territory owners (Watts et al. 2006, Crawford et al. 2015, Mayer et al. 2017c). Moreover, beavers breed in winter, and even if ice cover does not restrict their movement, water temperatures are low and lodges are vital for warmth and protection (Müller-Schwarze and Sun 2003). Seeking mating opportunities without a permanent lodge nearby is therefore risky (Sun et al. 2003). Since most individuals disperse in spring and summer (e.g. Hartman 1997), the number of floating (i.e. non-territory-holding) individuals during the mating season is likely very low due to harsh winter conditions. Thus, as compared to our study area, extensive snow cover during the mating season possibly restricts beaver movement in Kirov (Syrůčková et al. 2015), resulting in limited EPC opportunities. Moreover, we have used the data from 166 kits for parentage analysis, which is several times more than the data used by Russian study (n = 10; Syrůčková et al. 2015). Hence it is highly likely that the Syrůčková et al. (2015) failed to detect EPC due to low sample size.

Information on mate-guarding behavior in beavers is scarce (Sun et al. 2003, Busher et al. 2007). However, the strong seasonality and short duration of female estrus (Doboszynska and Zurowski 1983) should enable dominant males to either guard their female partner effectively or at least be able to observe her sufficiently to be aware of any extra-pair copulations (Sun et al. 2003). Mate guarding behavior is also proposed as an important factor in the evolution of monogamy in beavers (Busher et al. 2007). In addition, beavers conform to the dear-enemy phenomenon (Rosell and Bjørkøyli 2002), and older males have been shown to spend more time on land than on patrolling their water-centred territory borders (Graf et al. 2016), likely indicating less aggression towards their neighbours, i.e. potential extra-pair mates. In our study, the instances where the extra-pair mates could be identified (7 out of 9 cases), the father was a neighboring territory holder. This mirrors results from Crawford et al. (2008) in North American beavers, where most extra-pair young were also the result of mating between individuals from neighboring colonies. Moreover, none of the pairs produced more than one litter with extra-pair young, suggesting that EPP in Eurasian beavers may be the result of an occasional lapse in mate guarding ability by the aging social mate.

Beavers invest heavily into their territory in the form of construction activities such as building lodges, dams, and winter food caches (Busher et al. 2007). Especially, the adult male in a family group is actively involved in the construction behaviour (Busher et al. 2007). Additionally, in high-density populations, it is difficult to find vacant territories. Hence, it is not advantageous for a male to desert a female after an EPP occurrence, which may explain why beavers in our study did not divorce after an EPP event, but remained together until one of the partners died (Mayer et al. 2017a) mirroring observations in other mammals (e.g., meerkats (*Suricata suricatta*)(Leclaire

et al. 2013), but contrasting observations in many bird species (reviewed in Cezilly and Nager 1995).

Conclusions

We conclude that counter to previous suggestions (Syrůčková et al. 2015), EPC do occur in Eurasian beavers although at low frequency. Because EPP occurred only in pairs with older individuals, and older males typically show less aggression towards their neighbors, we suggest that EPC in Eurasian beavers is likely the result of a lapse in male mate guarding.

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References

- Bojarska, K., R. Kuehn, M. A. Gazda, N. J. Sato, Y. Okahisa, K. D. Tanaka, A. Attisano, R. Gula, K. Ueda, and J. Theuerkauf. 2018. Mating system and extra-pair paternity in the Fan-tailed Gerygone *Gerygone flavolateralis* in relation to parasitism by the Shining Bronze-cuckoo *Chalcites lucidus*. PLoS ONE 13:e0194059.
- Bonderud, E. S., K.A. Otter, T. M. Burg, K. L. D. Marini, and M. W. Reudnik. 2018. Patterns of extra-pair paternity in mountain chickadees. Ethology 124:378-386.
- Bowers, K. E., Forsman A. M., Masters B. S., Johnson B. G. P., Johnson L. S., Sakaluk S. K., Thompson C. F. 2015. Increased extra-pair paternity in broods of aging males and enhanced recruitment of extra-pair young in a migratory bird. Evolution 69:2533-2541
- Brotherton, P. N., J. M. Pemberton, P. E. Komers, and G. Malarky. 1997. Genetic and behavioural evidence of monogamy in a mammal, Kirk's dik-dik (*Madoqua kirkii*). Proceedings of the Royal Society of London B: Biological Sciences 264:675-681.
- Brotherton, P. N., and P. E. Komers. 2003. Mate guarding and the evolution of social monogamy in mammals. In U. Reichard, and C. Boesch (Eds.), *Monogamy: mating strategies and*

- 393 *partnerships in birds, humans and other mammals*. (pp. 42-58) Cambridge, Cambridge
394 University Press.
- 395
- 396 Busher, P. 2007. Social organization and monogamy in the beaver. In J. Wolff, and P. Sherman
397 (Eds.), *Rodent societies: an ecological and evolutionary perspective*. (pp. 280-290) Chicago,
398 Illinois, USA. University of Chicago Press.
- 399
- 400 Campbell R. D. 2010. Demography and life history of the Eurasian beaver *Castor fiber*.
401 University of Oxford.
- 402
- 403 Campbell, R. D., C. Newman, D. W. Macdonald, and F. Rosell. 2013. Proximate weather
404 patterns and spring green-up phenology effect Eurasian beaver (*Castor fiber*) body mass and
405 reproductive success: the implications of climate change and topography. *Global Change*
406 *Biology* 19:1311-1324.
- 407
- 408 Campbell, R. D., P. Nouvellet, C. Newman, D. W. Macdonald, and F. Rosell. 2012. The
409 influence of mean climate trends and climate variance on beaver survival and recruitment
410 dynamics. *Global Change Biology* 18:2730-2742.
- 411
- 412 Campbell, R. D., F. Rosell, C. Newman, and D. W. Macdonald. 2017. Age-related changes in
413 somatic condition and reproduction in the Eurasian beaver: Resource history influences onset of
414 reproductive senescence. *PloS One* 12:e0187484.
- 415
- 416 Campbell, R. D., F. Rosell, B. A. Nolet, and V. A. Dijkstra. 2005. Territory and group sizes in
417 Eurasian beavers (*Castor fiber*): echoes of settlement and reproduction? *Behavioral Ecology and*
418 *Sociobiology* 58:597-607.
- 419
- 420 Cezilly, F., and R. G. Nager. 1995. Comparative evidence for a positive association between
421 divorce and extra-pair paternity in birds. *Proceedings of the Royal Society of London B:*
422 *Biological Sciences* 262: 7-12
- 423
- 424 Cleasby, I. R., and S. Nakagawa. 2012. The influence of male age on within-pair and extra-pair
425 paternity in passerines. *Ibis* 154:318-324.
- 426
- 427 Clutton-Brock, T., and K. Isvaran. 2006. Paternity loss in contrasting mammalian societies.
428 *Biology Letters* 2:513-516.
- 429
- 430 Cockburn, A. 2006. Prevalence of different modes of parental care in birds. *Proceedings of the*
431 *Royal Society of London B: Biological Sciences* 273:1375-1383.
- 432

- 433 Cohas, A., and D. Allainé. 2009. Social structure influences extra-pair paternity in socially
434 monogamous mammals. *Biology Letters* 5:313-316.
- 435
- 436 Cohas, A., N. Yoccoz, A. Da Silva, B. Goossens, and D. Allainé. 2006. Extra-pair paternity in
437 the monogamous alpine marmot (*Marmota marmota*): the roles of social setting and female mate
438 choice. *Behavioral Ecology and Sociobiology* 59:597-605.
- 439
- 440 Cohas, A., N. G. Yoccoz, and D. Allainé. 2007. Extra-pair paternity in alpine marmots, *Marmota*
441 *marmota*: genetic quality and genetic diversity effects. *Behavioral Ecology and Sociobiology*
442 61:1081-1092.
- 443
- 444 Crawford, J. C., R. D. Bluett, and E. M. Schaubert. 2015. Conspecific aggression by beavers
445 (*Castor canadensis*) in the Sangamon river basin in central Illinois: correlates with habitat, age,
446 sex and season. *The American Midland Naturalist* 173:145-155.
- 447
- 448 Crawford, J. C., Z. Liu, T. A. Nelson, C. K. Nielsen, and C. K. Bloomquist. 2008. Microsatellite
449 analysis of mating and kinship in beavers (*Castor canadensis*). *Journal of Mammalogy* 89:575-
450 581.
- 451
- 452 Doboszynska, T., and W. Zurowski. 1983. Reproduction of the European beaver. *Acta Zoologica*
453 *Fennica*. 174:123-126.
- 454
- 455 Dobson, F. S., B. M. Way, and C. Baudoin. 2010. Spatial dynamics and the evolution of social
456 monogamy in mammals. *Behavioral Ecology* 21:747-752.
- 457
- 458 Emlen, S., and L. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems.
459 *Science* 197:215-223.
- 460
- 461 Foerster, K., K. Delhey, A. Johnsen, J. T. Lifjeld, and B. Kempenaers. 2003. Females increase
462 offspring heterozygosity and fitness through extra-pair matings. *Nature* 425:714.
- 463
- 464 Fukuda, K., H. Manabe, M. Sakurai, S. Dewa, A. Shinomiya, and T. Sunobe. 2017.
465 Monogamous mating system and sexuality in the gobiid fish, *Trimma marinae* (Actinopterygii:
466 Gobiidae). *Journal of Ethology* 35:121-130.
- 467
- 468 Graf, P. M., M. Mayer, A. Zedrosser, K. Hackländer, and F. Rosell. 2016. Territory size and age
469 explain movement patterns in the Eurasian beaver. *Mammalian Biology-Zeitschrift für*
470 *Säugetierkunde* 81:587-594.
- 471

- Griffith, S. C., I. P. Owens, and K. A. Thuman. 2002. Extra-pair paternity in birds: a review of interspecific variation and adaptive function. *Molecular Ecology* 11:2195-2212.
- Hartman, G. 1997. Notes on age at dispersal of beaver (*Castor fiber*) in an expanding population. *Canadian Journal of Zoology* 75:959-962.
- Herr, J., and F. Rosell. 2004. Use of space and movement patterns in monogamous adult Eurasian beavers (*Castor fiber*). *Journal of Zoology* 262:257-264.
- Hoogland, J. L. 2013. Why do female prairie dogs copulate with more than one male?— Insights from long-term research. *Journal of Mammalogy* 94:731-744.
- Huck, M., E. Fernandez-Duque, P. Babb, and T. Schurr. 2014. Correlates of genetic monogamy in socially monogamous mammals: insights from Azara's owl monkeys. *Proceedings of the Royal Society of London B: Biological Sciences* 281:20140195.
- Jennions, M. D., and M. Petrie. 2000. Why do females mate multiply? A review of the genetic benefits. *Biological Reviews* 75:21-64.
- Kalinowski, S. T., M. L. Taper, and T. C. Marshall. 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Molecular Ecology* 16:1099-1106.
- Kalinowski, S. T., M. L. Taper, and T. C. Marshall. 2010. Corrigendum. *Molecular Ecology* 19:1512-1512.
- Kempenaers, B., G. R. Verheyen, M. Van den Broeck, T. Burke, C. Van Broeckhoven, and A. Dhondt. 1992. Extra-pair paternity results from female preference for high-quality males in the blue tit. *Nature* 357:494.
- Kitchen, A. M., E. M. Gese, L. P. Waits, S. M. Karki, and E. R. Schauster. 2006. Multiple breeding strategies in the swift fox, *Vulpes velox*. *Animal Behaviour* 71:1029-1038.
- Krebs, J. R., and N. B. Davies. 2009. *Behavioural ecology: an evolutionary approach*. John Wiley & Sons.
- Leclaire, S., J. F. Nielsen, N. K. Thavarajah, M. Manser, and T. H. Clutton-Brock. 2013. Odour-based kin discrimination in the cooperatively breeding meerkat. *Biology Letters* 9:20121054.
- Lukas, D., and T. H. Clutton-Brock. 2013. The evolution of social monogamy in mammals. *Science* 341:526-530.

- Marshall, T., J. Slate, L. Kruuk, and J. Pemberton. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. *Molecular Ecology* 7:639-655.
- Mayer, M., F. Künzel, A. Zedrosser, and F. Rosell. 2017a. The 7-year itch: non-adaptive mate change in the Eurasian beaver. *Behavioral Ecology and Sociobiology* 71:32.
- Mayer, M., A. Zedrosser, and F. Rosell. 2017b. Couch potatoes do better: Delayed dispersal and territory size affect the duration of territory occupancy in a monogamous mammal. *Ecology and Evolution* 7:4347-4356.
- Mayer, M., A. Zedrosser, and F. Rosell. 2017c. Extra-territorial movements differ between territory holders and subordinates in a large, monogamous rodent. *Scientific Reports* 7:15261.
- Mayer, M., A. Zedrosser, and F. Rosell. 2017d. When to leave: the timing of natal dispersal in a large, monogamous rodent, the Eurasian beaver. *Animal Behaviour* 123:375-382.
- Moreno, J., J. G. Martinez, S. Gonzalez-Braojos, A. Cantarero, R. Ruiz-de-Castaneda, M. Precioso, and J. Lopez-Arrabe. 2015. Extra-Pair Paternity Declines with Female Age and Wing Length in the Pied Flycatcher. *Ethology* 121:501-512.
- Müller-Schwarze, D., and L. Sun. 2003. The beaver: natural history of a wetlands engineer. Cornell University Press.
- Nolet, B. A., and F. Rosell. 1994. Territoriality and time budgets in beavers during sequential settlement. *Canadian Journal of Zoology* 72:1227-1237.
- Parker, H., A. Zedrosser, and F. Rosell. 2017. Age-specific reproduction in relation to body size and condition in female Eurasian beavers. *Journal of Zoology* 302:236-243.
- Roemer, G. W., D. A. Smith, D. K. Garcelon, and R. K. Wayne. 2001. The behavioural ecology of the island fox (*Urocyon littoralis*). *Journal of Zoology* 255:1-14.
- Rosell, F., F. Bergan, and H. Parker. 1998. Scent-marking in the Eurasian beaver (*Castor fiber*) as a means of territory defense. *Journal of Chemical Ecology* 24:207-219.
- Rosell, F., and T. Bjørkøyli. 2002. A test of the dear enemy phenomenon in the Eurasian beaver. *Animal Behaviour* 63:1073-1078.
- Rosell, F., and B. Hovde. 2001. Methods of aquatic and terrestrial netting to capture Eurasian beavers. *Wildlife Society Bulletin*:269-274.

- 552 Rosell, F., and L. Sun. 1999. Use of anal gland secretion to distinguish the two beaver species
553 *Castor canadensis* and *C. fiber* Wildlife Biology 5:119-123.
- 554
- 555 Rosell, F., A. Zedrosser, and H. Parker. 2010. Correlates of body measurements and age in
556 Eurasian beaver from Norway. European Journal of Wildlife Research 56:43-48.
- 557
- 558 Schubert, M., C. Schradin, H. G. Rödel, N. Pillay, and D. O. Ribble. 2009. Male mate guarding
559 in a socially monogamous mammal, the round-eared sengi: on costs and trade-offs. Behavioral
560 Ecology and Sociobiology 64:257-264.
- 561
- 562 Senn, H., R. Ogden, T. Cezard, K. Gharbi, Z. Iqbal, E. Johnson, N. Kamps-Hughes, F. Rosell,
563 and R. McEwing. 2013. Reference-free SNP discovery for the Eurasian beaver from restriction
564 site-associated DNA paired-end data. Molecular Ecology 22:3141-3150.
- 565
- 566 Senn, H., R. Ogden, C. Frosch, A. Syrůčková, R. Campbell-Palmer, P. Munclinger, W. Durka, R.
567 H. Kraus, A. P. Saveljev, and C. Nowak. 2014. Nuclear and mitochondrial genetic structure in
568 the Eurasian beaver (*Castor fiber*)—implications for future reintroductions. Evolutionary
569 Applications 7:645-662.
- 570
- 571 Smith, J. M. 1978. *The evolution of sex*. Cambridge, Cambridge University Press.
- 572 Steyaert, S. M., A. Zedrosser, and F. Rosell. 2015. Socio-ecological features other than sex affect
573 habitat selection in the socially obligate monogamous Eurasian beaver. Oecologia 179:1023-
574 1032.
- 575
- 576 Sun, L. 2003. Monogamy correlates, socioecological factors, and mating systems in beavers. In
577 U. Reichard, and C. Boesch (Eds.) *Monogamy: Mating strategies and partnerships in birds,*
578 *humans and other mammals*. (pp.138-146). Cambridge, UK: Cambridge University Press.
- 579
- 580 Svendsen, G. E. 1989. Pair formation, duration of pair-bonds, and mate replacement in a
581 population of beavers (*Castor canadensis*). Canadian Journal of Zoology 67:336-340.
- 582
- 583 Syrůčková, A., A. P. Saveljev, C. Frosch, W. Durka, A. A. Savelyev, and P. Munclinger. 2015.
584 Genetic relationships within colonies suggest genetic monogamy in the Eurasian beaver (*Castor*
585 *fiber*). Mammal Research 60:139-147.
- 586
- 587 Tarof, S. A., P. M. Kramer, J. Tautin, and B. J. Stutchbury. 2011. Effects of known age on male
588 paternity in a migratory songbird. Behavioral Ecology 23:313-321.
- 589
- 590 Tregenza, T., and N. Wedell. 2000. Genetic compatibility, mate choice and patterns of parentage:
591 invited review. Molecular Ecology 9:1013-1027.

- Trivers, R. 1972. Parental investment and sexual selection. Biological Laboratories, Harvard University Cambridge, MA.
- Uller, T., and M. Olsson. 2005. Multiple copulations in natural populations of lizards: evidence for the fertility assurance hypothesis. Behaviour 142:45-56.
- Vedder, O., J. Komdeur, M. van der Velde, E. Schut, and M. J. Magrath. 2011. Polygyny and extra-pair paternity enhance the opportunity for sexual selection in blue tits. Behavioral Ecology and Sociobiology 65:741-752.
- Watts, D. P., M. Muller, S. J. Amsler, G. Mbabazi, and J. C. Mitani. 2006. Lethal intergroup aggression by chimpanzees in Kibale National Park, Uganda. American Journal of Primatology 68:161-180.
- Westneat, D. F., and I. R. Stewart. 2003. Extra-pair paternity in birds: causes, correlates, and conflict. Annual Review of Ecology, Evolution, and Systematics 34:365-396.
- Wilsson, L. 1971. Observations and experiments on the ethology of the European beaver (*Castor fiber L.*): A study in the development of phylogenetically adapted behaviour in a highly specialized mammal. Umea, Sweden: Svenska Jägareförbundet.
- Zhao, M., C. Li, W. Zhang, H. Wang, Z. Luo, Q. Gu, Z. Gu, C. Liao, and H. Wu. 2016. Male pursuit of higher reproductive success drives female polyandry in the Omei treefrog. Animal Behaviour 111:101-110.

Figure 1

Eurasian beaver (*Castor fiber*) in southeast Norway

Our study species Eurasian beaver (*Castor fiber*) in southeast Norway. (photo credits : Priyank Sharad Nimje)



Figure 2

Relationship between the age of genetic mothers as well as the age of their social mates, and the proportion of extra-pair young (EPY)

Relationship between the age of genetic mothers as well as the age of their social mates, and the proportion of extra-pair young (EPY) found in Eurasian beavers from southeast Norway based on data collected from 1998 – 2016.

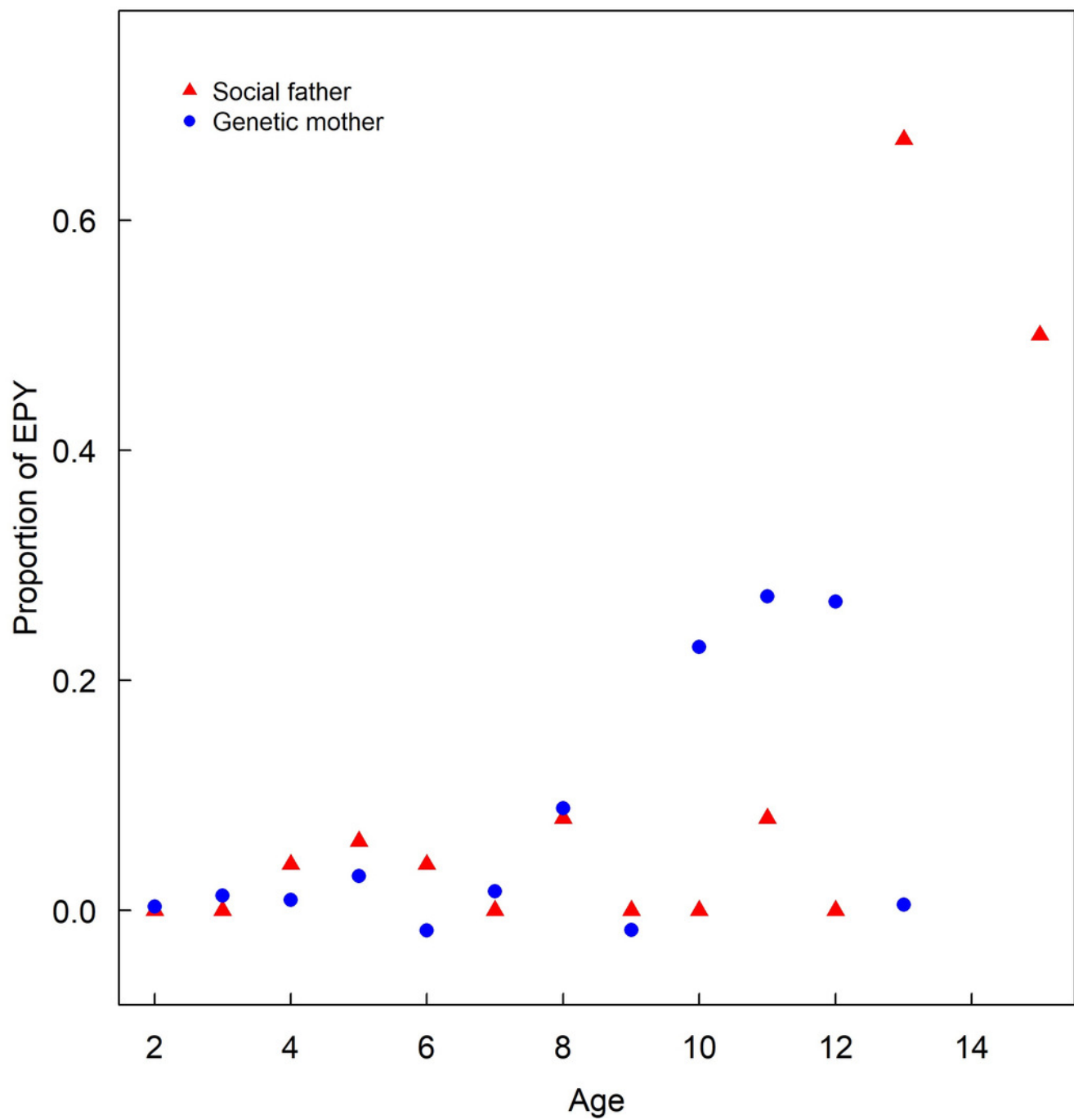


Figure 3

Relationship between the age of genetic mothers as well as the age of their social mates, and the number of offspring included in this study.

Relationship between the age of genetic mothers as well as the age of their social mates, and the number of offspring in Eurasian beaver from southeast Norway based on the data collected from 1998-2016.

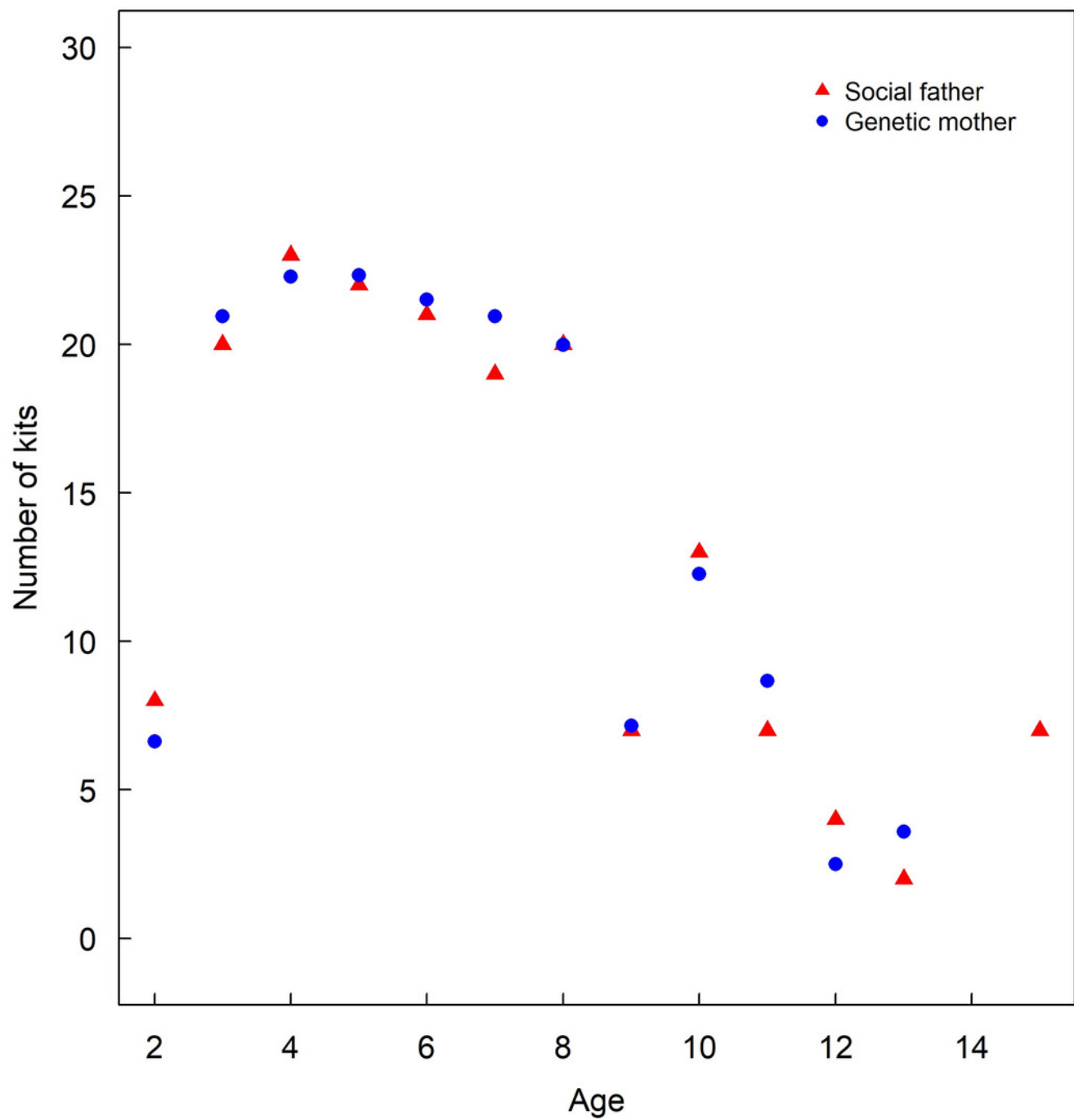


Table 1 (on next page)

Summary statistics of 27 single nucleotide polymorphisms (SNPs) from a Norwegian population of Eurasian beavers (*Castor fiber*)

Table 1. Summary statistics of 27 single nucleotide polymorphisms (SNPs) from a Norwegian population of Eurasian beavers (*Castor fiber*) based on samples collected from 1998 - 2016.

k = number of alleles, N = number of samples, H_{obs} = observed heterozygosity, H_{exp} = expected heterozygosity, PIC = polymorphic information content, NE-1P = average nonexclusion probability for one candidate parent, NE-2P = average nonexclusion probability for one candidate parent given the genotype of a known parent of the opposite sex, HW = significance of deviation from Hardy-Weinberg equilibrium, NS: not significant

Locus	SNP	<i>k</i>	<i>N</i>	<i>H</i> _{obs}	<i>H</i> _{exp}	PIC	NE-1P	NE-2P	HW
D9	9267	2	352	0.432	0.426	0.335	0.910	0.833	NS
E9	102408	2	351	0.464	0.500	0.375	0.875	0.813	NS
E10	102426	2	353	0.470	0.501	0.375	0.875	0.813	NS
E11	105238	2	354	0.410	0.376	0.305	0.930	0.848	NS
F1	109525	2	355	0.428	0.501	0.375	0.875	0.813	NS
F2	112139	2	354	0.390	0.391	0.314	0.924	0.843	NS
F3	11809	2	354	0.427	0.477	0.363	0.887	0.819	NS
F5	30128	2	352	0.395	0.425	0.334	0.910	0.833	NS
F6	34297	2	351	0.382	0.424	0.334	0.910	0.833	NS
F7	34680	2	352	0.435	0.496	0.373	0.877	0.814	NS
F8	40318	2	347	0.522	0.500	0.375	0.875	0.813	NS
F9	44292	2	351	0.342	0.387	0.313	0.925	0.843	NS
F10	45990	2	352	0.227	0.228	0.201	0.974	0.899	NS
F11	50941	2	352	0.466	0.501	0.375	0.875	0.813	NS
F12	55280	2	354	0.466	0.479	0.364	0.885	0.818	NS
G1	56140	2	352	0.321	0.296	0.252	0.956	0.874	NS
G2	57669	2	354	0.492	0.475	0.362	0.887	0.819	NS
G3	58111	2	337	0.433	0.466	0.357	0.892	0.822	NS
G4	61846	2	350	0.457	0.485	0.367	0.883	0.816	NS
G5	63983	2	354	0.291	0.330	0.275	0.946	0.863	NS
G6	67449	2	352	0.415	0.426	0.335	0.910	0.833	NS
G7	7071	2	353	0.354	0.340	0.282	0.942	0.859	NS
G8	73032	2	356	0.199	0.219	0.195	0.976	0.903	NS
G10	79605	2	326	0.426	0.443	0.344	0.902	0.828	NS
G11	81918	2	349	0.370	0.398	0.319	0.921	0.841	NS
H1	95943	2	351	0.430	0.466	0.357	0.892	0.821	NS
H2	96886	2	352	0.509	0.500	0.375	0.875	0.813	NS
Mean				0.406	0.424	0.331	0.071	0.008	NS

Table 2 (on next page)

Results from paternity analyses of 166 young from 48 pairs of a socially monogamous Eurasian beaver population in Norway based on data collected from 1998 – 2016.

Table 2. Results from paternity analyses of 166 young from 48 pairs of a socially monogamous Eurasian beaver population in Norway based on data collected from 1998 – 2016. N_{EPP} is the number of kits where there is evidence of extra-pair paternity, names of the genetic fathers are given in brackets.

Couple No.	Colony	Female	Male	Length pairbond	N _{offspring} (N _{litters})	N _{EPP}
1	Lunde 1a	Trude	Jon	1999 - 2011	1	-
2		Waltraut	Priyank	2014 - 2016*	3 (2)	-
3	Lunde 2a	Birgit	Ørjan	1999 - 2005	2 (2)	1 (Frode)
4	Lunde 2b	Blondi	Frode	1999 - 2005	3 (2)	-
5	Lunde 3a	Randi	Grønn	1999 - 2004	4 (3)	-
6		Suzanne	Loran	2007 - 2010	6 (2)	-
7	Lunde 4a	Hanne	Jørn	1999 - 2005	5 (5)	-
8		Malena	Rory	2011 - 2016*	2 (1)	2 (Darwin)
9	Lunde 4c	Laura	Darwin	2014 - 2016*	1	-
10	Lunde 4b/2a	Gyda	Lasse	2009 - 2016*	12 (5)	-
11		Bjørk	Carl	1999 - 2000	2 (1)	-
12	Lunde 5a	Stina	Carl	2002 - 2004	4 (3)	-
13		Stina	Easy	2006 - 2009	1	-
14	Lunde 5b	Sonja	Bram	2005 - 2007	2 (1)	-
15		Stina	Chris	2010 - ?	1	-
16		Yasmin	Rudolf	2014 - 2016*	2 (1)	-
17	Evju	Frøydis	Jan Helge	1998 - 1999	1	-
18		Demi	Oddi	2008 - 2009	1	-
19	Håtveit	Kathrin	Homer	2009 - 2011	2 (2)	-
20		Gabi	Homer	2013 - 2016	1	-
21	Gvarv upper	Asun	Øyvind	2015 - 2016*	1	-
22	Gvarv middle	Ikea	Klumpen	2003 - 2014	12 (6)	-
23	Gvarv lower	Hazel	Konrad	2006 - 2011	6 (2)	-
24		Hazel	Paddy	2012 - 2016*	5 (4)	1(unknown)
25	Norsjø 1	Sofie	Tåkehode	1998 - 2005	9 (4)	-
26		Else Beth	Stuart	2004 - 2007	3 (2)	-
27	Patmos 0	Hanne			1	-
28		Synnøve	Jan Marc	2008 - 2011		-
29		Live	Manuel	2012 - 2015	4 (2)	-
30	Patmos 1	Apple	Morten	2016 - 2016*	2 (1)	-
31		Anne Lise	Terje	2003 - 2011	5 (4)	1(unknown)
32		Live	Caesar	2015 - 2016*	3 (1)	-
33	Patmos 2a	Olive	Tommy	2003 - 2012	8 (4)	2 (Mini)
34		Nanna	Mini	2014	1	-
35	Patmos 2b	Athena	Anders	2016 - 2016*	1	-
36		Torunn	Moses	2006 - 2016	7 (3)	-
37	Patmos 3a	Torunn	Pablo	2016 - 2016*	1	-
		Christina	Ola By	2004 - 2013	6 (4)	1 (Mini)

38	Bråfjorden A	Leslie	Laurits	2011 - 2016*	9 (4)	-
39	Bråfjorden B	Lona	Moritz	2007 - 2014	7 (5)	-
40	Lille Patmos	Helga	Kjartan	2005 - 2007	2 (1)	-
41		Lise	Kjartan	2008 - 2009	3 (2)	-
42		Ida	Kjartan	2010 - ?	2 (1)	-
43	Patmos 4	Tanja	Horst	2005 - 2013	2 (2)	-
44	Patmos 5	Rosa	Dino	2005 - 2009	2 (1)	-
45		Tanja	Dino	2010 - ?	2 (1)	-
46		Tanja	Thomas	2014 - 2016*	2 (2)	1 (Edwin)
47	Patmos 6	Karin	Ludwin	2008 - 2013	3 (1)	-
48		Åse	Edwin	2014 - 2016*	1	-

1

2 * The pair is still together

Table 3(on next page)

Details from the seven Eurasian beaver pairs where evidence of extra-pair paternity was found, based on data collected from 1998 – 2016 in Southeast Norway.

Table 3. Details from the seven Eurasian beaver pairs where evidence of extra-pair paternity was found, based on data collected from 1998 – 2016 in Southeast Norway. The age of the male, female and extra-pair mate is the age at the time of the conception of extra-pair young. Most ages are minimum ages, as the individuals were first trapped as an adults (≥ 3 years).

Couple No.	Colony	Length pairbond _{EPP}	Length pairbond _{Total}	N _{pair} offspring	N _{EPP}	Birth year EPP kit	Age _{Female}	Age _{Male}	Age _{EPM}	Fate
3	Lunde 2a	>2	>6	1	1	2000	> 5	> 5	> 5	Male died 2005, no more kits. Female moved together with father of EPP kit
8	Lunde 4a	5	5*	0	2	2016	> 8	> 8	6	*Couple still together
24	Gvarv lower	2	4*	4	1	2014	> 10	6	NA	*Couple still together
30	Patmos 1	6	8	4	1	2009	11	11	NA	Both killed by hunter in 2011, no more kits
32	Patmos 2a	9	9	6	2	2012	> 10	> 13	9	Both died fall/winter 2012, father of EPP kit took over territory with new female
37	Patmos 3a	9	9	5	1	2012	> 13	> 15	9	Male died fall 2012
46	Patmos 5	1	2*	1	1	2015	> 11	> 4	> 7	*Couple still together