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The 7-year itch: non-adaptive mate change in the Eurasian beaver

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Abstract

Mate change in socially monogamous species can be explained by adaptive and non-adaptive hypotheses. Adaptive hypotheses describe a mate change as a strategy to correct for initial mate choice and to improve reproductive success: the 'incompatibility' hypothesis states that mate change is initiated by both mates, whereas in the 'better option' hypothesis, one partner initiates the mate change. In contrast, non-adaptive hypotheses predict mate change to be independent from previous reproduction: the 'forced divorce' hypothesis suggests that mate change is initiated by an incoming individual and the 'obligate mate change' hypothesis states that the mate change occurs after the accidental death of a partner. We investigated these hypotheses in the socially monogamous Eurasian beaver (Castor fiber), using data from a long-term study in southeast Norway between 1998 and 2014. Generally, the mate change occurred in the seventh year of a partnership and the staying individual re-

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paired with a younger, incoming individual. The fate of the replaced individual was mostly unknown. Resident individuals had a decreased reproductive success with increasing age but gained no benefits from a mate change in terms of reproduction. Thus, we reject the adaptive hypotheses as cause of mate change. Our results support non-adaptive mate change hypotheses, most likely the 'forced divorce' hypothesis and to a lower degree the 'obligate mate change' hypothesis.

Significance statement

We investigated the causes of mate change in the Eurasian beaver, a long-lived, monogamous mammal living in family groups. We found that mate change was not initiated by a member of the mated couple but rather by the intrusion of an incoming individual as suggested by the 'forced divorce' hypothesis. Additionally, mate change was partly caused by the accidental loss of a partner. Mean reproductive success did not change after a mate change but with increasing age of the resident individual suggesting senescence. Together with a study on Alpine marmots, this is one of the first studies investigating mate change in mammals.

Keywords Forced divorce · Mammals · Monogamy · Pair bond · Reproductive success

Introduction

A mating system is defined as socially monogamous when females and males form exclusive pairs for at least one reproductive event or breeding season and as genetically monogamous when the members of a pair share exclusive parentage (Reichard and Boesch 2003). Only a minority of socially monogamous animal species have a unique, holistic, monogamous lifetime partnership, and generally individuals will accept a new mate if the first mate dies or is lost otherwise, i.e. serial or sequential social monogamy (Wickler and Seibt 1983).

Mate choice is a critical factor for an individual's reproductive success, especially in monogamous species. However, individuals may be forced to pair with a suboptimal mate because the process of mate selection is competitive and limited in time (Luttbeg 2002). Behavioural strategies to adjust for initial mate choice are extra-pair copulation (EPC) (Møller 1988; Forstmeier et al. 2014) or adaptive mate change, i.e. divorce. Hypotheses regarding the cause of divorce (Table 1) have been investigated particularly in birds (Choudhury 1995). The 'incompatibility' hypothesis suggests that a pair with poor genetic or behavioural compatibility divorces to pair with more compatible mates. The decision to divorce is assumed to be mutual by both sexes, and divorce is more likely to occur early in a partnership and in pairs with low reproductive success (Choudhury 1995). As a consequence of mating with a new mate, both members of the original pair should increase their reproductive success after divorce (Choudhury 1995; Ens et al. 1996). In contrast, the 'better option' hypothesis states that only one partner initiates a divorce, and only this individual will improve its reproductive success after re-pairing with a higher quality mate (Ens et al. 1993; Choudhury 1995). Both hypotheses suggest that divorce is an adaptive strategy to correct for initial mate choice. However, Taborsky and Taborsky (1999) introduced a non-adaptive hypothesis, the 'forced divorce' hypothesis, where divorce is proposed to be the outcome of intra-sexual competition. The divorce is caused by the intrusion of a third individual who outcompetes the same-sex member of a pair. This process is independent of previous reproductive success, which should not improve for the resident after pairing with the new mate (Taborsky and Taborsky 1999). Studies in birds suggest that 'forced divorce' is most common in populations at or close to carrying capacity when competition for mates increases (Taborsky and Taborsky 1999; Heg et al. 2003; Jeschke et al. 2007). Another non-adaptive hypothesis, the 'obligate mate change' hypothesis, states that the

accidental death of a partner, i.e. widowing (e.g. due to hunting), leads to a divorce (Lardy et al. 2011).

Divorce in monogamous species has been reported for invertebrates (Beltran et al. 2008), fish (van Breukelen and Draud 2005), birds (Heg et al. 2003; Jeschke et al. 2007; Dreiss and Roulin 2014), rodents (Svendsen 1989) and primates (Palombit 1994). However, to our knowledge, the only study testing hypotheses about the causes of mate change in mammals was carried out on the Alpine marmot (*Marmota marmota*) finding evidence for the 'forced divorce' hypothesis (Lardy et al. 2011).

Here, we investigated the causes of mate change in a socially monogamous mammal, the Eurasian beaver (Castor *fiber*), by comparing the 'incompatibility', the 'better option', the 'forced divorce' and the 'obligate mate change' hypotheses (Table 1) using data from a long-term study in southeast Norway. For the 'incompatibility' hypothesis, we predicted that a mate change occurs early in a partnership and is dependent on previous reproductive success. Therefore, reproductive success in pairs where no mate change occurs was expected to be higher than in pairs that later experienced a mate change. In addition, we tested whether the age difference between the members of the dominant pair affected the probability of a mate change, predicting that pairs with a larger age difference were more likely to divorce as shown in humans (Kalmijn and Poortman 2006). For the 'better option' hypothesis, we predicted an improved reproductive success of the resident after re-pairing with a new mate. For the 'forced divorce' hypothesis, we predicted that the mate change is independent of reproductive success and will not increase after repairing. In order to successfully challenge a resident dominant beaver, we also expected the incoming individual to be of similar or greater body mass than the individual replaced by the divorce. For the 'obligate mate change' hypothesis, we predicted that the body mass of the incoming individual would be independent of replaced individual's mass and that the mate change would be independent of the reproductive success. Further, we hypothesised

Table 1 Hypotheses and then predectors regarding mate change in socially monoganious species
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Hypothesis	Definition	Predictions
'Better option'	Mate change is initiated by one pair member	Mate change is beneficial (better mate, better territory, improved reproduction) only for the individual initiating the mate change
'Incompatibility'	Mate change is initiated by both pair members and dependent on previous reproductive success	Mate change occurs early in the partnership, and reproductive success improves for both individuals after the mate change
'Forced divorce'	Mate change is independent from previous reproductive success and initiated by an intruder	No improvement of reproductive success after the mate change
'Obligate mate change'	Mate change is caused by the accidental death of the replaced individual and is independent from previous reproductive success	No improvement of reproductive success after the mate change

that the mate change rate (i.e. the proportion of mate change in a population) would be related to a fluctuating population density.

Material and methods

Study species

The Eurasian beaver is a large, socially monogamous rodent. It is similar to the North American beaver (Castor canadensis); both species live in family groups consisting of the dominant pair and offspring from the current and previous years (Sun 2003). Beavers are considered obligate monogamous as they exhibit a high degree of biparental care (Wilsson 1971; Kleiman 1977; Sharpe and Rosell 2003). Juvenile beavers stay in their natal territory until they reach sexual maturity and usually disperse thereafter to establish a territory of their own (Svendsen 1989; Hartman 1997; McNew et al. 2005) but may remain within the natal territory as old as 7 years (Mayer et al. 2016). Only the dominant pair reproduces with copulation taking place between late January and February and one to four kits usually born around mid-May (Parker and Rosell 2001; Sun 2003). Pairs form year round, but pair formation was shown to peak (56 % of all known pairs) in September, October and November in a population of North American beavers (Svendsen 1989). Once paired, beavers remain a couple for long periods (Wilsson 1971; Svendsen 1989; Sun 2003). Due to this behaviour, beavers are assumed to be genetically monogamous (Sun 2003; Busher 2007). However, the first molecular study investigating paternity in North American beavers revealed the presence of EPC (Crawford et al. 2008). In contrast, Syrůčková et al. (2015) did not find any evidence of EPC in a Eurasian beaver population. Dominant adults are highly territorial and both sexes participate in scent marking and territorial defence (Jenkins and Busher 1979; Rosell and Nolet 1997). Intruders are treated aggressively and territorial combat can result in serious or even fatal injuries (Nolet and Rosell 1994; Crawford et al. 2015).

Study area and data collection

The study area consisted of the three rivers Straumen (59° 29' N, 09° 153' E), Gvarv (59° 386' N, 09° 179' E) and Sauar (59° 444' N, 09° 307' E) in Telemark County, southeast Norway (Campbell et al. 2012). The population density was saturated in all three rivers (Campbell et al. 2012) with adjacent territories and no unoccupied stretch of river in between (Herr and Rosell 2004). Hunting pressure in the study area was considered to be low (Campbell et al. 2012). Because wolves (*Canis lupus*) and bears (*Ursus arctos*) were functionally absent, and

lynx (*Lynx lynx*) occurred in low densities, predation pressure was also considered to be low (Rosell and Sanda 2006).

Beavers were monitored since 1998 via an extensive livetrapping program during spring (March-June) and fall (August-October) each year (Stevaert et al. 2015). Capture took place at night from a motor boat with a landing net, and beavers were immobilized in a cloth sack during handling without medical sedation (Rosell and Hovde 2001). The colour of the anal gland secretion was used to determine the sex of individuals (Rosell and Sun 1999), and beavers were weighed to the nearest 500 g. For individual identification, all beavers were tagged with a microchip and a unique combination of plastic or metal ear tags (Campbell et al. 2012). Individuals were confirmed as dominant (being the reproducing individual) from genetic paternity tests (FR, unpublished data) and via multiple capture and sighting events and lactation in females. Unless dominant individuals disappeared or died, they were assumed to maintain their status (most individuals were captured annually). Individuals that had newly dispersed into a territory were considered as dominant if the previously dominant territory holder of the same sex disappeared at the same time (Campbell et al. 2012) and based on positive paternity tests. Annual reproductive success was defined as the number of kits in a given year and was based on the number of trapped and observed kits plus the number of unmarked yearlings captured in the following year (i.e. kits missed the previous year) (Campbell et al. 2013). Also, we recorded family group sizes every year (after the kits had emerged from the lodge) based on captures and observations. It was not possible to record data blind because our study involved focal animals in the field.

Data preparation

We defined mate change as when one of the dominant individuals (hereafter the replaced) was no longer observed in the territory or was found dead and another individual of the same sex (the successor) had obtained the dominant breeding position together with the remaining individual (the resident). We defined the timing of mate change as the year *t* when the replaced was last observed in its territory and the start of the new pair bond between the successor and the resident in the year when the successor was first observed (which could be either year *t* (4 cases) or t + 1 (21 cases)).

For individuals first trapped as kit or yearling, exact age determination was possible. For older individuals (≥ 2 years), a minimum age was assigned when first captured based on body mass (Rosell et al. 2010) with beavers being classified as minimum 2-year-olds when they had a mass ≥ 17 and ≤ 19.5 kg or as minimum 3 years when >19.5 kg at the time of first capture (e.g. a beaver captured for the first time in 1999 with 18 kg was classified as minimum 2 years old and therefore, when captured again in 2002, it was classified as

minimum 5 years old). We tested if the assigned age was a good estimate for individuals of uncertain age (replaced = 15, residents = 15, successor = 6) and compared them with individuals of known age (replaced = 5, residents = 5, successor = 14) separately for each group using a Mann-Whitney U test. There was no difference between the age of replaced individuals (9.66 \pm 3.39 (mean \pm standard error) years vs. 9.40 \pm 4.22, p = 0.965), residents (8.93 \pm 3.71 vs. 8.00 \pm 2.00 years, p = 0.597) and successors (4.67 \pm 4.18 vs. 4.43 \pm 2.77 years, p = 0.802). Therefore, we considered the assigned age as a good estimate and used it for further analyses. To test for age differences, the age of all groups (replaced, resident and successor) was assigned to year *t*.

The mass measurements were taken in either year t or t - 1for the replaced and year t or t + 1 for the successor but with a maximum difference of 1 year between replaced and successor. To correct for the year difference (if captured in different years), we estimated mean annual growth increments separately for male and female beavers using a generalized linear mixed model (GLMM) using the package lme4 (Bates et al. 2015) following Campbell (2010). Both models were based on mass measurements from beavers of known ages (males = 210 observations, females = 137 observations, Fig. S1). The models were carried out with an identity link, mass as dependent variable, age and age² as fixed effects and the individual ID as random effect. We then used these mean growth increments (Fig. S1) to correct the mass of the replaced or the resident to the year t, based on the estimates of the models. Because beavers gain mass during summer (Smith and Jenkins 1997), all measurements were additionally adjusted to the same day of the year (Julian day 182, first of July), using an estimated daily growth rate of 0.012 kg for adults and 0.021 kg for subordinates (Campbell 2010). Population density was measured annually as the mean number of individuals per family group separately for each study site.

Data analysis

For our analyses, we only used individuals of known and finished duration of territory occupation. To test the 'incompatibility' hypothesis, we compared the annual reproductive success of pairs that experienced a mate change only using the original pair (i.e. the resident with the replaced, n = 19 pairs, 108 pair years) with the annual reproductive success of pairs that remained together for their whole life (n = 7 pairs, 46 pair years). We used a GLMM with the occurrence of mate change in a given year (yes vs. no) as dependent variable and the pair as random effect to account for multiple observations. We included as fixed effects the annual reproductive success (as measure of compatibility), the age difference between the male and female of the dominant pair (as another measure of compatibility, predicting that pairs with a greater

age difference would be less compatible) and the pair bond length (to test the prediction that a mate change should occur early in a partnership).

To test the 'better option' and 'forced divorce' hypotheses, we tested if the annual reproductive success of the resident increased ('better option') or was unchanged ('forced divorce') when mated with the first (the replaced) and the second partner (the successor) in pairs that experienced a mate change (n = 19 mate changes and 38 pairs (18 residents, from which one had three mates), 166 pair years). We used a GLMM with a negative binomial error distribution of the response variable, using the R package glmmADMB (Bolker et al. 2012) in order to correct for a non-normal distribution of the annual reproductive success and to correct for zero inflation (O'hara and Kotze 2010). The annual reproductive success was the dependent variable, and the resident was used as the random effect. The mate order (mate 1 vs. mate 2), the age difference within the pair (for the original and the new pair, respectively), the pair bond length, the age of the resident individual (to control for possible age effects) and the interaction between the mate order and the sex of the resident (to test if the mate change only had advantages for one sex) were included as fixed effects.

To further test the 'forced divorce' hypothesis, we compared the body mass between the successor and the replaced (which was known in 11 cases) using a paired Mann-Whitney U test; and we investigated whether replaced individuals disappeared due to conspecific aggression ('forced divorce') or accidents ('obligate mate change').

We calculated the annual mate change rate for each year and study site by dividing the number of mate changes by the number of observed pairs. To check if the mate change rate (dependent variable) was related to the adult population density (independent variable, kits and yearlings were excluded assuming that they would not challenge a resident), we used a linear mixed-effect model (LME) using the R package *lmerTest* (Kuznetsova et al. 2013) with the study site as random effect. The mate change rate was square-root transformed to meet assumptions of normality and homogeneity of variance (Hu 2007).

The fixed effects/independent variables used in all analyses were not correlated (all Pearson *r* coefficient < 0.6) and variance inflation factor values were <3 (Zuur et al. 2010). Model selection was carried out using Akaike's Information Criterion (AIC_c values) (Burnham and Anderson 2002; Arnold, 2010). We used the dredge function in the R package *MuMIn* (Barton 2013) to create candidate models including all possible combinations of fixed effects (no interactions were included due to the small sample sizes). Parameters that included zero within their 95 % confidence interval (CI) were considered as uninformative (Arnold 2010). All analyses were conducted in R 3.1.1 (R Core Team 2015). Mean values are given with standard error (SE).

Results

Sixty-two beaver pairs consisting of 101 dominant individuals were observed in 30 territories from 1998 to 2014 (44 partnerships were terminated at this time). During this period, 73 individuals had one mate, 16 individuals had two mates, for eight individuals the number of mates was uncertain and four individuals had more than two mates with a maximum of four mates.

For 25 pairs the partnership ended in a mate change, 19 pairs were still together at the end of this study, in 11 cases both members of the pair were replaced by a new dominant pair (of these replaced pairs, seven pairs stayed together for life, i.e. had only one partner, and four had had another partner previously) and seven cases were uncertain due to a lack of information on the end of the partnership or the new mate. Human-caused mortality (hunting and car accidents) accounted for 20 % of the mate changes (five cases out of 25). These cases, uncertain cases and cases with incomplete information, were not used for further analyses. The average annual mate change rate was 7.03 ± 10.35 % and tended to decrease negatively with increasing adult population density ($\beta \pm SE = -1.093 \pm 0.546$, p = 0.056). When including kits and yearlings in the calculation of the population density, this trend became significant $(\beta \pm SE = -0.743 \pm 0.326, p = 0.030, Fig. 1).$

The average pair bond length of all terminated partnerships in the study area was 4.73 ± 3.04 years (range = 1– 14 years, n = 44). Pairs that remained together for life had an average pair bond length of 6.57 ± 2.07 years (range = 4–9 years, n = 7). In pairs that experienced a mate change, the partnership with the first mate lasted on average significantly longer than with the second mate (paired Mann-Whitney U test = 6.25 ± 3.53 vs. 3.06 ± 1.84 years, n = 19, p = 0.007, Fig. 2).



Fig. 1 Predicted relationship between the population density (measured as the annual average number of individuals per family group including kits and yearlings separately for each river) and the annual mate change rate (%) for our Eurasian beaver population in southeast Norway, 1998–2014



Fig. 2 Box plot showing the pair bond length (in years) with the first and the second partner (n = 19 pairs) for data of Eurasian beavers in southeast Norway, 1998–2014. The box plots show median values, 25th and 75th percentile and the range of the data

For pairs that stayed together for life (n = 7), the average annual probability to reproduce was 0.39 ± 0.49 and they had on average 0.59 ± 0.86 kits per year (median = 0). In pairs that experienced a mate change and where we had information on annual reproductive success (n = 19 mate changes), the average annual probability to reproduce was 0.38 ± 0.49 with the first mate (on average 0.60 ± 0.86 kits per year, median = 0) and 0.28 ± 0.45 with the second mate (on average 0.45 ± 0.86 kits per year, median = 0).

In the 20 mate changes (that were not human-caused), nine males and 11 females were replaced. The fate of the replaced was unknown in 17 cases, in two cases the replaced was found dead and in one case it established a new territory and re-paired with a new individual (Table 2). From the 20 successors, 11 were subdominant before intruding the new territory, two were previously dominant and seven came from outside the study area (Table 2). No successor was born in the same family group as the replaced individual.

Testing the 'incompatibility' hypothesis

There was no age difference (in the year the partnership ended) between individuals of pairs where both partners were simultaneously replaced as compared to individuals of pairs that later experienced a mate change (9.00 \pm 2.63 vs. 9.61 \pm 2.90 years, Mann-Whitney U test: p = 0.412). The occurrence of a mate change was not related to the annual reproductive success, the age difference within pairs or the pair bond length but was best explained by the intercept alone model (n = 26 pairs, 154 pair years, Table 3).

Testing the 'better option' and 'forced divorce' hypotheses

The age difference between the male and the female of the original pair was significantly smaller than the age difference

Table 2Overview of male and female replaced individuals andincoming individuals (successors) involved in mate change in aEurasian beaver population in southeast Norway, 1998–2014

	Male	Female	Total
Replaced	9	11	20
Fate			
Unknown	8	9	17
Dead	1	1	2
Re-paired	0	1	1
Successor	9	11	20
Status			
Unknown	3	4	7
Subdominant	5	6	11
Dominant	1	1	2

For the replaced individuals, the fate is shown after the mate change. For the successors, the social status before intruding is shown

between the remaining individual of the original pair and its second mate (1.63 \pm 2.34 vs. 4.74 \pm 4.07 years, Mann-Whitney U test: p = 0.005). Annual reproductive success decreased with increasing age of the resident but was independent from the mate order, the age difference between the original and the new pair, the pair bond length and the sex of the resident (n = 19 mate changes, 38 pairs, 166 pair years, Table 3). Replaced individuals were significantly older than successors in the year the mate change occurred (10.21 \pm 2.70 vs. 6.00 \pm 3.43 years, n = 20, p < 0.001, Fig. 3), but there was no significant difference in body mass (replaced = 21.43 \pm 2.52 kg

Table 3The five mostparsimonious and the full model(based on AIC weights) for theanalysis of the probability of matechange and the variation in annualreproductive success in theEurasian beaver based on datacollected between 1998 and 2014in southeast Norway



Fig. 3 Box plot showing the age (in years) of the replaced and the successor (n = 38 individuals) in the year the mate change occurred for data of Eurasian beavers in southeast Norway, 1998–2014. The box plots show median values, 25th and 75th percentile and the range of the data including an outlier (*dot*)

vs. successor = 19.44 ± 3.35 kg, n = 11 mate changes, p = 0.240).

Discussion

Our study showed that mate change in the Eurasian beaver was independent of previous reproductive success and that reproductive success did not increase after a mate change. Therefore, we reject the adaptive 'incompatibility' and 'better option' hypotheses. Our results support the non-adaptive

Probability of mate change								
Model	Fixed effects	Estimate ± SE	LCI	UCI	df	AIC _c	ΔΑΙϹ	AIC weight
1	Intercept	14.09 ± 2.57	NA	NA	152	26.90	0.00	0.399
2	Age difference					28.90	1.99	0.147
3	Pair bond length				151	29.00	2.06	0.142
4	Annual reproductive success				151	29.00	2.08	0.141
5	Age difference + pair bond length				150	31.00	4.05	0.053
Full	Age difference + pair bond length + annual reproductive success					33.10	6.19	0.018
Annual r	eproductive succ	ess						
Model	Fixed effects	Estimate \pm SE	LCI	UCI	df	AIC _c	ΔAIC	AIC weight
1	Resident age	-0.12 ± 0.04	-0.20	-0.04	162	328.40	0.00	0.299
2	Age difference + resident age				161	330.10	1.70	0.128
3	Partner + resident age				161	330.40	2.04	0.108
4	Pair bond length + resident age				161	330.50	2.12	0.104
5	Partner + resident age + partner × resident sex				159	331.00	2.68	0.078
Full	Age difference + pair bond length + partner + resident age + partner × resident sex				157	334.60	6.24	0.013

The remaining degrees of freedom (*df*), the AIC_c and Δ AIC are given for all models. For the best model (model 1), parameters are given with estimates (β), standard error (SE) and lower (LCI) and upper (UCI) 95 % confidence intervals

hypotheses, i.e. the 'forced divorce', and to a lesser degree the 'obligate mate change' hypotheses.

Adaptive hypotheses

When evaluating the causes of mate change, it is crucial to identify which mate initiated the mate change. We only had data on the reproductive success after a mate change for residents, however never for the replaced, because in most cases the replaced was assumed to be dead or to have dispersed outside the study area.

The 'incompatibility' hypothesis predicts that in cases when both partners initiate a mate change simultaneously, then such a change should occur early in a partnership and should be more likely for pairs with low reproductive success (Ens et al. 1996). In our study, mate change occurred on average in the seventh year of a partnership and was independent from previous annual reproductive success. The average pair bond length in our study was 4.95 years as compared to 2.5 years in a North American beaver population (Svendsen 1989). These differences might be due to different population densities or environmental factors in the respective populations.

Year-round territorial species are generally assumed to exhibit strong site fidelity, as the benefits of holding a territory are expected to be greater than the costs of being paired with a low-quality or incompatible mate (Morton et al. 2000). For example, buff-breasted wrens (Thrvothorus leucotis) were more faithful to their territories than to their mates (Gill and Stutchbury 2006). This might be especially the case in saturated populations with only very few available territories and a high intruder pressure, such as our study population (Mayer et al. 2016), and is also in line with Lardy et al. (2011) who suggested that deserting a territory would be very costly for a dominant individual. Hence, we consider it unlikely that a one or both members of the pair initiated the partner change and left its territory. Nevertheless, secondary dispersal might occur as shown in a North American beaver population (Sun et al. 2000) but is considered unlikely as only one dominant individual (replaced) re-established after a mate change and because of the high population density in our area.

If the resident initiated the mate change, it presumably would gain some benefits (e.g. an improved reproductive success) according to the 'better option' hypothesis (Ens et al. 1993; Choudhury 1995). As residents in our study were never observed changing their territory, the benefits should be directly related to the quality of the new mate. For example, in the endoparasite *Schistosoma mansoni*, the divorce rate increased when females were given the chance to increase genetic dissimilarity through re-pairing (Beltran et al. 2008). However, the mitochondrial DNA haplotype variation is zero in beavers from southeast Norway (Durka et al. 2005), and there is also little variation in nuclear fingerprinting profiles (Ellegren et al. 1993). In addition, the reproductive success in our population is lower as compared to German and Russian beaver populations with greater genetic diversity (Heidecke 1984; Saveljev and Milishnikov 2002; Halley 2011). This suggests that reproductive benefits achieved by a mate change may be low due to genetic causes.

Non-adaptive hypotheses

Our results show that mate change was not due to low reproductive success with the initial partner, and it did not increase after mating with a new partner. This suggests that mate change in the Eurasian beaver is non-adaptive, similar to alpine marmots (*M. marmota*) (Lardy et al. 2011) and common guillemots (*Uria aalge*) (Jeschke et al. 2007).

The reproductive success decreased with increasing age of the resident suggesting senescence.

We found no difference in body mass between the replaced and the successor. In our study population, mass gain stagnated approximately at age 6 in both sexes and decreased in males around age 8 (but not in females), indicating senescence (replaced individuals were on average 10 years old). Moreover, movement patterns of dominant beavers in our study area changed over time, with older individuals spending more time on land (Graf et al. 2016), which might also indicate senescence. Hu and Morse (2004) showed that in male crab spiders (Misumena vatia) of similar body mass, young individuals were more successful in encounters than old ones. Also, middle-aged male song sparrows (Melospiza melodia) were more successful in expanding and regaining territories as compared to younger or older individuals (Arcese 1989). This indicates that, after a certain point, competitive ability decreases with increasing age, which may result in competitive advantages for incoming younger successors. We found two dead individuals with bite marks and captured four injured individuals with bite marks suggesting territorial fights between replaced and successor. Moreover, most of the adult beavers we captured had tail scars, indicating frequent conspecific disputes (MM, unpublished result), which is in line with Crawford et al. (2015) who showed that conspecific aggression is widespread in North American beavers. Additionally, the population densities in our area were very high (Campbell et al. 2012) possibly leading to a high intruder pressure. Combined, these findings support the 'forced divorce' hypothesis suggesting that younger beavers intrude a territory and take it over after a physical dispute.

We found some evidence that the mate change rate increased with decreasing population density. A reduction in the population density was likely caused by increased mortality, either via intraspecific competition in line with the 'forced divorce' hypothesis or via other causes of mortality (e.g., hunting, accidents), resulting in the widowing of the resident, i.e. the 'obligate mate change' hypothesis. Although considered low (Campbell et al. 2012), the hunting pressure in our area might be higher than suspected as cryptic hunting was reported in many wildlife species (Gavin et al. 2010; Liberg et al. 2012) and might be in fact a driver of the beaver population in Telemark. This is partly supported by the high number of unknown fates of replaced beavers (which likely did not undergo secondary dispersal (Campbell et al. 2005)) and because 20 % of all mate changes were due to legal hunting. Population densities would be expected to decrease with increasing hunting pressure, and Parker et al. (2002) showed that adult and pregnant beavers were more likely to be shot. Consequently, the mate change rate could increase with increasing hunting pressure due to widowing, supporting the 'obligate mate change' hypothesis. In wolves (Canis lupus), Milleret et al. (2016) showed that the majority of pair dissolutions were related to human-caused mortalities, such as legal control actions and cryptic hunting. Also, Forslund and Larsson (1991) found that mate change in barnacle geese (Branta leucopsis) was the consequence of the (likely accidental) loss of one partner.

In conclusion, we found support for the prediction of Lardy et al. (2011) that adaptive hypothesis of mate change should be poorly supported in monogamous long-lived species that hold a territory year-round. Our study adds to the small number of studies suggesting non-adaptive hypotheses as the cause of mate change in monogamous mammals.

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Conflict of interest The authors declare that they have no conflict of interest.

References

- Arcese P (1989) Territory acquisition and loss in male song sparrows. Anim Behav 37:45–55
- Arnold TW (2010) Uninformative parameters and model selection using Akaike's information criterion. J Wildlife Manage 74:1175–1178
- Barton K (2013) MuMIn: multi-model inference. R package version 1.9.5., https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf

- Bates D, Maechler M, Bolker B, Walker S, Christensen RHB, Singmann H, Dai B, Eigen C, Rcpp L (2015) Package 'lme4'. https://cran.rproject.org/web/packages/lme4/lme4.pdf
- Beltran S, Cézilly F, Boissier J (2008) Genetic dissimilarity between mates, but not male heterozygosity, influences divorce in schistosomes. PLoS One 3(10):e3328. doi:10.1371/journal.pone.0003328
- Bolker B, Skaug H, Magnusson A, Nielsen A (2012) Getting started with the glmmADMB package. http://glmmadmb.r-forge.r-project. org/glmmADMB.pdf
- Burnham K, Anderson D (2002) Model selection and multimodel interference: a practical-theoretical approach. Springer, Berlin
- Busher P (2007) Social organization and monogamy in the beaver. In: Wolff JO, Sherman PW (eds) Rodent societies: an ecological and evolutionary perspective. University of Chicago Press, Chicago, pp 280–290
- Campbell RD (2010) Demography and life history of the Eurasian beaver *Castor fiber*. DPhil thesis, University of Oxford
- Campbell RD, Newman C, Macdonald DW, Rosell F (2013) Proximate weather patterns and spring green-up phenology effect Eurasian beaver (*Castor fiber*) body mass and reproductive success: the implications of climate change and topography. Glob Chang Biol 19: 1311–1324
- Campbell RD, Nouvellet P, Newman C, Macdonald DW, Rosell F (2012) The influence of mean climate trends and climate variance on beaver survival and recruitment dynamics. Glob Change Biol 18:2730– 2742
- Campbell RD, Rosell F, Nolet BA, Dijkstra VA (2005) Territory and group sizes in Eurasian beavers (*Castor fiber*): echoes of settlement and reproduction? Behav Ecol Sociobiol 58:597–607
- Choudhury S (1995) Divorce in birds: a review of the hypotheses. Anim Behav 50:413–429
- Crawford JC, Bluett RD, Schauber EM (2015) Conspecific aggression by beavers (*Castor canadensis*) in the Sangamon river basin in central Illinois: correlates with habitat, age, sex and season. Am Midl Nat 173:145–155
- Crawford JC, Liu Z, Nelson TA, Nielsen CK, Bloomquist CK (2008) Microsatellite analysis of mating and kinship in beavers (*Castor canadensis*). J Mammal 89:575–581
- Dreiss A, Roulin A (2014) Divorce in the barn owl: securing a compatible or better mate entails the cost of re-pairing with a less ornamented female mate. J Evol Biol 27:1114–1124
- Durka W, Babik W, Ducroz JF, Heidecke D, Rosell F, Samjaa R, Saveljev AP, Stubbe A, Ulevicius A, Stubbe M (2005) Mitochondrial phylogeography of the Eurasian beaver *Castor fiber* L. Mol Ecol 14:3843–3856
- Ellegren H, Hartman G, Johansson M, Andersson L (1993) Major histocompatibility complex monomorphism and low levels of DNA fingerprinting variability in a reintroduced and rapidly expanding population of beavers. P Natl Acad Sci USA 90:8150–8153
- Ens B, Choudhury S, Black J (1996) Mate fidelity and divorce in monogamous birds. In: Black JM (ed) Partnerships in birds: the study of monogamy. Oxford University Press, Oxford, pp 344–401
- Ens BJ, Safriel UN, Harris MP (1993) Divorce in the long-lived and monogamous oystercatcher, *Haematopus ostralegus*: incompatibility or choosing the better option? Anim Behav 45:1199–1217
- Forslund P, Larsson K (1991) The effect of mate change and new partner's age on reproductive success in the barnacle goose, *Branta leucopsis*. Behav Ecol 2:116–122
- Forstmeier W, Nakagawa S, Griffith SC, Kempenaers B (2014) Female extra-pair mating: adaptation or genetic constraint? Trends Ecol Evol 29:456–464
- Gavin MC, Solomon JN, Blank SG (2010) Measuring and monitoring illegal use of natural resources. Conserv Biol 24:89–100
- Gill SA, Stutchbury BJ (2006) Long-term mate and territory fidelity in neotropical buff-breasted wrens (*Thryothorus leucotis*). Behav Ecol Sociobiol 61:245–253

- Graf PM, Mayer M, Zedrosser A, Hackländer K, Rosell F (2016) Territory size and age explain movement patterns in the Eurasian beaver. Mamm Biol 81:587–594
- Halley DJ (2011) Sourcing Eurasian beaver *Castor fiber* stock for reintroductions in Great Britain and Western Europe. Mamm Rev 41:40–53
- Hartman G (1997) Notes on age at dispersal of beaver (*Castor fiber*) in an expanding population. Can J Zool 75:959–962
- Heg D, Bruinzeel LW, Ens BJ (2003) Fitness consequences of divorce in the oystercatcher, *Haematopus ostralegus*. Anim Behav 66:175–184
- Heidecke D (1984) Untersuchungen zur Ökologie und Populationsentwicklung des Elbebibers (*Castor fiber albicus* Matschie, 1907). I: Biologische und populationsökologische Ergebnisse. Zool Jahrb Abt Syst Oekol Geogr Tiere 111:-41
- Herr J, Rosell F (2004) Use of space and movement patterns in monogamous adult Eurasian beavers (*Castor fiber*). J Zool 262:257–264
- Hu HH, Morse DH (2004) The effect of age on encounters between male crab spiders. Behav Ecol 15:883–888
- Hu S (2007) Akaike information criterion. Center for Research in Scientific Computation. North Carolina State University, Raleigh, NC
- Jenkins SH, Busher PE (1979) Castor canadensis. Mamm Species 120:1-8
- Jeschke JM, Wanless S, Harris MP, Kokko H (2007) How partnerships end in guillemots *Uria aalge*: chance events, adaptive change, or forced divorce? Behav Ecol 18:460–466
- Kalmijn M, Poortman A-R (2006) His or her divorce? The gendered nature of divorce and its determinants. Eur Sociol Rev 22:201–214
- Kleiman DG (1977) Monogamy in mammals. Q Rev Biol 52:39–69
- Kuznetsova A, Brockhoff PB, Christensen RHB (2013) ImerTest: tests for random and fixed effects for linear mixed effect models (Imer objects of Ime4 package). R package version 2, https://cran.rproject.org/web/packages/ImerTest/ImerTest.pdf
- Lardy S, Cohas A, Figueroa I, Allainé D (2011) Mate change in a socially monogamous mammal: evidences support the "forced divorce" hypothesis. Behav Ecol 22:120–125
- Liberg O, Chapron G, Wabakken P, Pedersen HC, Hobbs NT, Sand H (2012) Shoot, shovel and shut up: cryptic poaching slows restoration of a large carnivore in Europe. Proc R Soc Lond B 279:910–915
- Luttbeg B (2002) Assessing the robustness and optimality of alternative decision rules with varying assumptions. Anim Behav 63:805–814
- Mayer M, Zedrosser A, Rosell F (2016) When to leave: the timing of natal dispersal in a large, monogamous mammal, the Eurasian beaver. Anim Behav 123: 375-382
- McNew J, Lance B, Woolf A (2005) Dispersal and survival of juvenile beavers (*Castor canadensis*) in southern Illinois. Am Midl Nat 154: 217–228
- Milleret C, Wabakken P, Liberg O, Åkesson M, Flagstad Ø, Andreassen HP, Sand H (2016) Let's stay together? Intrinsic and extrinsic factors involved in pair bond dissolution in a recolonizing wolf population. J Anim Ecol 86:43–54
- Morton ES, Derrickson KC, Stutchbury BJ (2000) Territory switching behavior in a sedentary tropical passerine, the dusky antbird (*Cercomacra tyrannina*). Behav Ecol 11:648–653
- Møller AP (1988) Female choice selects for male sexual tail ornaments in the monogamous swallow. Nature 332:640–642
- Nolet BA, Rosell F (1994) Territoriality and time budgets in beavers during sequential settlement. Can J Zool 72:1227–1237
- O'Hara RB, Kotze DJ (2010) Do not log-transform count data. Method Ecol Evol 1:118–122
- Palombit R (1994) Dynamic pair bonds in hylobatids: implications regarding monogamous social systems. Behaviour 128:65–101

- Parker H, Rosell F (2001) Parturition dates for Eurasian beavers *Castor fiber*: when should spring hunting cease? Wildlife Biol 7:237–241
- Parker H, Rosell F, Hermansen TA, Sørløkk G, Stærk M (2002) Sex and age composition of spring-hunted Eurasian beaver in Norway. J Wildlife Manage: 1164–1170
- R Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, https://cran.r-project.org/doc/manuals/fullrefman.pdf
- Reichard UH, Boesch C (eds) (2003) Monogamy: mating strategies and partnerships in birds, humans and other mammals. Cambridge University Press, Cambridge
- Rosell F, Hovde B (2001) Methods of aquatic and terrestrial netting to capture Eurasian beavers. Wildlife Soc B 29:269–274
- Rosell F, Nolet BA (1997) Factors affecting scent-marking behavior in Eurasian beaver (*Castor fiber*). J Chem Ecol 23:673–689
- Rosell F, Sanda J (2006) Potential risks of olfactory signaling: the effect of predators on scent marking by beavers. Behav Ecol 17:897–904
- Rosell F, Sun L (1999) Use of anal gland secretion to distinguish the two beaver species *Castor canadensis* and *C. fiber*. Wildlife Biol 5:119– 123
- Rosell F, Zedrosser A, Parker H (2010) Correlates of body measurements and age in Eurasian beaver from Norway. Eur J Wildlife Res 56:43– 48
- Saveljev A, Milishnikov A (2002) Biological and genetic peculiarities of cross-composed and aboriginal beaver populations in Russia. Acta Zool Lituanica 12:397–402
- Sharpe F, Rosell F (2003) Time budgets and sex differences in the Eurasian beaver. Anim Behav 66:1059–1067
- Sikes RS, Gannon WL (2011) Guidelines of the American Society of Mammalogists for the use of wild mammals in research. J Mammal 92:235–253
- Smith DW, Jenkins SH (1997) Seasonal change in body mass and size of tail of northern beavers. J Mammal 78:869–876
- Steyaert S, Zedrosser A, Rosell F (2015) Socio-ecological features other than sex affect habitat selection in the socially obligate monogamous Eurasian beaver. Oecologia 179:1023–1032
- Sun L (2003) Monogamy correlates, socioecological factors, and mating systems in beavers. In: Reichard UH, Boesch C (eds) Monogamy: mating strategies and partnerships in birds, humans and other mammals. Cambridge University Press, Cambridge, pp 138–146
- Sun L, Müller-Schwarze D, Schulte BA (2000) Dispersal pattern and effective population size of the beaver. Can J Zool 78:393–398
- Svendsen GE (1989) Pair formation, duration of pair-bonds, and mate replacement in a population of beavers (*Castor canadensis*). Can J Zool 67:336–340
- Syrůčková A, Saveljev AP, Frosch C, Durka W, Savelyev AA, Munclinger P (2015) Genetic relationships within colonies suggest genetic monogamy in the Eurasian beaver (*Castor fiber*). Mamm Res 60:139–147
- Taborsky B, Taborsky M (1999) The mating system and stability of pairs in kiwi *Apteryx spp.* J Avian Biol 30:143–151
- van Breukelen NA, Draud M (2005) The roles of male size and female eavesdropping in divorce in the monogamous convict cichlid (Archocentrus nigrofasciatus, Cichlidae). Behaviour 142:1023– 1035
- Wickler W, Seibt U (1983) Monogamy: an ambiguous concept. In: Bateson P (ed) Mate choice. Cambridge University Press, Cambridge, pp 33–50
- 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. Svenska Jägareförbundet, Uppsala
- Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. Method Ecol Evol 1:3–14