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Faithful or not: direct and indirect effects of climate on extra-pair paternities in a population of Alpine marmots

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Despite being identified an area that is poorly understood regarding the effects of climate change, behavioural responses to climatic variability are seldom explored. Climatic variability is likely to cause large inter-annual variation in the frequency of extra-pair litters produced, a widespread alternative mating tactic to help prevent, correct or minimize the negative consequences of sub-optimal mate choice. In this study, we investigated how climatic variability affects the inter-annual variation in the proportion of extra-pair litters in a wild population of Alpine marmots. During 22 years of monitoring, the annual proportion of extra-pair litters directly increased with the onset of earlier springs and indirectly with increased snow in winters. Snowier winters resulted in a higher proportion of families with sexually mature male subordinates and thus, created a social context within which extra-pair paternity was favoured. Earlier spring snowmelt could create this pattern by relaxing energetic, movement and time constraints. Further, deeper snow in winter could also contribute by increasing litter size and juvenile survival. Optimal mate choice is particularly relevant to generate adaptive genetic diversity. Understanding the influence of environmental conditions and the capacity of the individuals to cope with them is crucial within the context of rapid climate change.

1. Introduction

The impact of climatic variability on ecological processes is widely recognized [1–3]. Shifts in species phenology [4] and distribution [5] are now considered two universal responses to global warming [6]. While both ecological and demographic responses have received substantial attention, behavioural responses to climatic variations have been seldom investigated [7], despite being stressed as an area that is poorly understood regarding the effects of climate change [8].

Climate fluctuations have been suggested to favour the evolution of alternative mating tactics in order to help prevent, correct or minimize the negative consequences of sub-optimal mate choice [9]. Engaging in extra-pair copulation is a widespread alternative mating tactic [10,11] and a comparative analysis has revealed a positive association between the variability and predictability of annual climatic cycles with the prevalence of extra-pair paternity (EPP) among species of socially monogamous birds [9]. Large inter-annual variations in the frequency of EPP have also been observed within populations [12,13], and climatic variability is likely to be at the origin of these variations. For example, in sand lizards (*Lacerta agilis*), a higher incidence of multiple paternity is observed in warmer years [14] due to an increase in individual opportunities for mate searching in these years [15]. Similarly, in the yellow-bellied marmot (*Marmota flaviventris*), multiple paternities are common in years of low snow depth during the reproductive period [16]. Ecological factors are indeed expected to directly affect the costs and benefits of engaging in extra-pair

mating for all individuals in a population [17] through the modulation of two critical determinants of this behaviour: the availability of extra-pair partners and the capacity of an individual to access available extra-pair partners [10]. Although so far neglected, ecological factors can also impact these costs and benefits indirectly. For instance, family-living species present higher EPP rates than pair-living species [18,19], particularly when group size is large [20,21]. As climatic conditions can affect population density [22], they could modulate the number of available males and, as a consequence, could indirectly impact annual EPP rates.

Here, we investigated how climatic variations directly and indirectly affect the inter-annual variation in the proportion of extra-pair litters (EPLs) observed over 22-years in a population of Alpine marmots (*M. marmota*). Alpine marmots are territorial and socially monogamous mammals living in family groups of two to 16 individuals composed of a dominant couple, sexually mature (more than or equal to 2 years) and immature subordinates of both sexes (1 year), and pups [23]. Alpine marmots hibernate from mid-October to early April and mating occurs shortly after the end of the hibernation. Although socially monogamous, EPPs are prevalent [24–26] and show high inter-annual variation (between 0 and 43% of litters contain extra-pair young, EPY). Climatic conditions are likely to have direct and/or indirect effects on inter-annual variation in EPLs. With regard to direct climatic effects, we expected that the annual proportion of EPLs depends on environmental variations during and immediately after hibernation. As observed for the yellow-bellied marmots [16], we first expected winter conditions to have a relatively weaker influence on the annual proportion of EPLs than spring conditions. Second, we expected a strong positive effect from earlier springs on the annual proportion of EPLs because females and males could have more time to find mates, and their movements are easier in the absence of snow despite the better body condition of females when snow is abundant during winter [27]. As regards to indirect effects, we predicted snowy winters to indirectly increase the annual proportion of EPLs through its delayed effect on the social structure of the population. Indeed, in Alpine marmots, as in other cooperative breeders [19], the propensity of females to produce EPLs is partly explained by social factors and, more specifically, increases with the number of sexually mature male subordinates present in the family group [26]. In our population, snowy winters lead to increased litter size [27] and pup survival [28]; and consequently to an increase in the proportion of families with sexually mature male subordinates 2 years later [28], a social context favouring an increase in the annual proportion of EPLs.

2. Material and methods

(a) Field methods

Marmots were monitored from 1992 to 2013 in La Grande Sassièr Nature Reserve (2340 m.a.s.l., French Alps, 45°29' N, 65°90'). Marmots belonging to 31 family groups were captured annually, from mid-April to mid-July using two-door live-capture traps (see [29] for details). Traps were placed near the entrance of the main burrows of each group to assign trapped individuals to their family. Once captured, individuals were tranquilized with Zolétil 100, sexed, aged, and their social status (dominant or subordinate) was determined. Body size allowed four age classes

to be distinguished: juvenile, yearling, 2-year old and adult individuals. The social status was determined through examination of sexual characteristics (scrotum for dominant males and teats for dominant females) and was confirmed by behavioural observations. Scent-marking behaviour was used to discriminate subordinates and dominants because only dominants actively mark and defend their territory [30]. Trapped individuals were marked with a transponder and a numbered ear-tag, placed on the right ear of females, and the left ear of males. An additional coloured plastic ear-tag was placed on the opposite ear of dominant individuals. In addition, we collected hair for genetic analyses.

Each year, the composition of each family group was determined by combining individuals' capture histories with intensive daily observations (see [29] for details). The number of pups was estimated from additional daily observations (see [26]) and, almost all pups were trapped within the 3 days after the first emergence from the natal burrow.

(b) Parentage analyses

All captured individuals were genotyped at 16 microsatellite loci and parentage analyses were performed by both exclusion analyses and paternity analyses conducted with CERVUS 3.0.3 [31]. The genotypes of each pup and of the supposed parents (dominant pair) were compared to assign parentage. The effective mother always corresponded to the putative mother except in one case where one mismatch at one locus between the supposed mother and one of her pups was found. A pup was then considered as within-pair young (WPY) if no mismatch was observed with the genotype of the dominant male and, otherwise, as EPY. A litter was considered as a within-pair litter (WPL) when no pup mismatched with the genotype of the dominant male and, otherwise, as an EPL. Further details of the genotyping method and parentage analyses can be found in 36 and in the electronic supplementary material, appendix S1.

(c) Environmental covariates

(i) Social covariates

Social environment is known to affect the mating tactics of Alpine marmots. More specifically, the female propensity to produce EPLs increases with the number of sexually mature subordinate males in the family [26]. To characterize the social context at the annual scale, we thus used the annual proportion of families having sexually mature male subordinates, a good indicator of social changes in the population structure [28]. Moreover, in the field, the presence/absence of subordinate males in each family is more reliably assessed and over a larger number of families than their exact number.

(ii) Climatic covariates

Local weather variables were used to identify by which mechanisms climate influences the annual proportion of EPLs in Alpine marmots. We focused on two different seasons with a potential impact on marmot mating tactics: (i) winter between 1 December to 31 March, during the hibernation period preceding the mating season (hereafter snow depth at t) and 2 years before (hereafter snow depth at $t-2$); and (ii) spring at emergence from hibernation during the mating season. Winter was characterized by the average snow depth recorded from the weather station of Tignes (73 296 400, located less than 5 km away from the study site). Spring was characterized by the Normalized Differential Vegetation Index (NDVI), extracted in the second half of April (15 April–1 May) from the NOAA/NASA with a 8×8 km resolution (AVHRR) from 1990 to 2000, and a 1×1 km resolution (MODIS) from 2001 to 2013. The NDVI in the second half of April measures the timing of snowmelt (hereafter snowmelt at t)

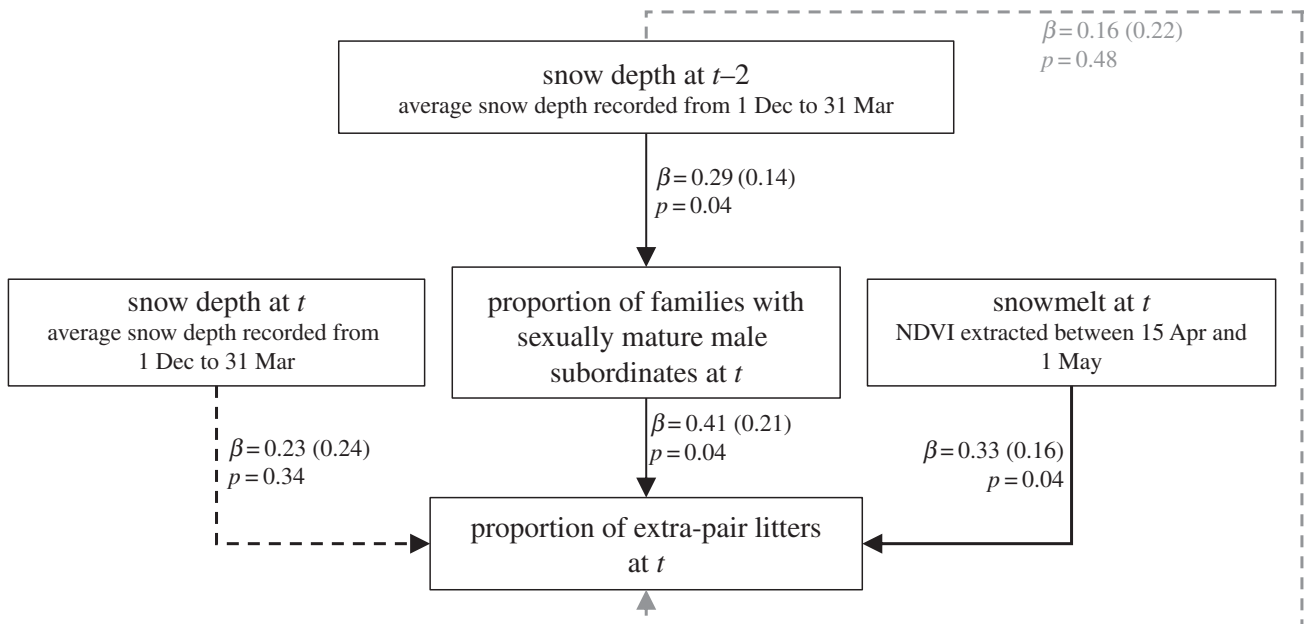


Figure 1. Effects of social and climatic variations acting directly and indirectly on the annual proportion of litters with extra-pair offspring of Alpine marmots at La Grande Sassi re (French Alps) between 1992 and 2013. The grey arrows represent the independent claim, while the black ones represent the hypothesized causal relationships. Solid lines indicate statistically supported effects, and dashed lines, non-statistically supported effects. The β values are given with their standard errors in parentheses.

because the vegetation onset correlates closely with snowmelt in mountainous environments [32]. We used the NDVI values in the second half of April to match the mating season [33]. High NDVI values indicate early spring and thus early snowmelt. No correlation was evidenced between snow depth and April NDVI ($r_{\text{Pearson}} = -0.35$, $t = -1.67$, d.f. = 20, $p = 0.11$).

(d) Statistical analyses

From 1992 to 2013, the dominant individuals (82 females and 104 males) and all offspring ($N = 864$) from 251 litters (from three litters in 1992 to 18 in 2008 with a mean of 11.41 litters by year) were known and genotyped. Additionally, for each year, the proportion of families with mature male subordinates in the population was known.

To investigate whether environmental variables (i.e. snow depth at t and $t-2$ and snowmelt at t) could directly and/or indirectly impact on the annual proportion of EPLs, we performed a confirmatory path analysis *sensu* [34] using the D-step procedure [35] (see electronic supplementary material, appendix S3 for details). First, we constructed a generalized path model corresponding to the following hypothesized causal relationships: (i) snowy winters (snow depth at $t-2$) indirectly affect the proportion of EPLs by affecting the proportion of families with sexually mature male subordinates, (ii) snowmelt at t and (iii) snow depth at t directly affect the occurrence of EPLs (figure 1). Second, we constructed the basis set by considering all possible conditional independence claims, filtering out exogenous pairs of variables and refining based on previous knowledge of the biological system. We ended up with a basis set containing a single independence claim (figure 1): the annual proportion of EPLs at t is independent of snow depth at $t-2$. Third, we tested for the validity of the hypothesized causal relationships using the C-statistic [35]. Once the generalized path model validated, the path coefficients were finally obtained by fitting two generalized linear models (GLMs) with a logit link function. In the first GLM, we entered the annual number of EPLs as the response variable and the annual number of litters produced as the binomial denominator. The proportion of families with sexually mature male subordinates, the snow depth at t and the snowmelt at t were entered as explanatory variables. In the second GLM, we

entered the annual number of families with sexually mature male subordinates at year t as the response variable and the corresponding number of families as the binomial denominator; the snow depth at $t-2$ being entered as the explanatory variable.

Because the annual variations in the proportion of EPLs result from mating decisions taken at the individual level, we also investigated how environmental variations affect the propensity of females to produce EPLs (details in electronic supplementary material, appendix S4).

The path analyses were conducted using the R v. 3.1.2 [36] and the package piecewiseSEM [37]. Unless otherwise stated, all social and climatic variables were standardized in order to compare their effect size. Parameter estimates are given as mean \pm s.e. and on the logit scale.

3. Results

Among the 251 litters, 34 were EPLs and 217 were WPLs with the proportion of EPLs varying from 0% in 1992, 1996, 2004, 2007 and 2012 to 43% in 2000. The path analysis confirmed that the proportion of EPLs in a given year was independent of the snow depth 2 years before ($\beta = 0.16 \pm 0.22$, $Z = 0.71$, $p = 0.48$) and prevented us from rejecting the hypothesized causal relationships proposed in figure 1 (C-value = 1.47, d.f. = 2, $p = 0.48$). The annual proportion of EPLs increased in years where more families had sexually mature male subordinates ($\beta = 0.41 \pm 0.21$, $Z = 2.01$, $p = 0.04$; figure 2a). It further increased to a slightly lesser extent when snow melted earlier ($\beta = 0.33 \pm 0.16$, $Z = 2.10$, $p = 0.04$; figure 2b) while the snow depth during the preceding winter had no direct effect on the annual proportion of EPLs ($\beta = 0.23 \pm 0.24$, $Z = 0.96$, $p = 0.34$). Finally, snow depth two winters before indirectly increased the annual proportion of EPLs via its positive impact on the proportion of families with sexually mature male subordinates ($\beta = 0.29 \pm 0.14$, $Z = 2.01$, $N = 22$, $p = 0.04$; figure 3). Snow depth at $t-2$, snowmelt at t and the presence of subordinates in a family affected the propensity of females to produce EPLs leading to the pattern evidenced in

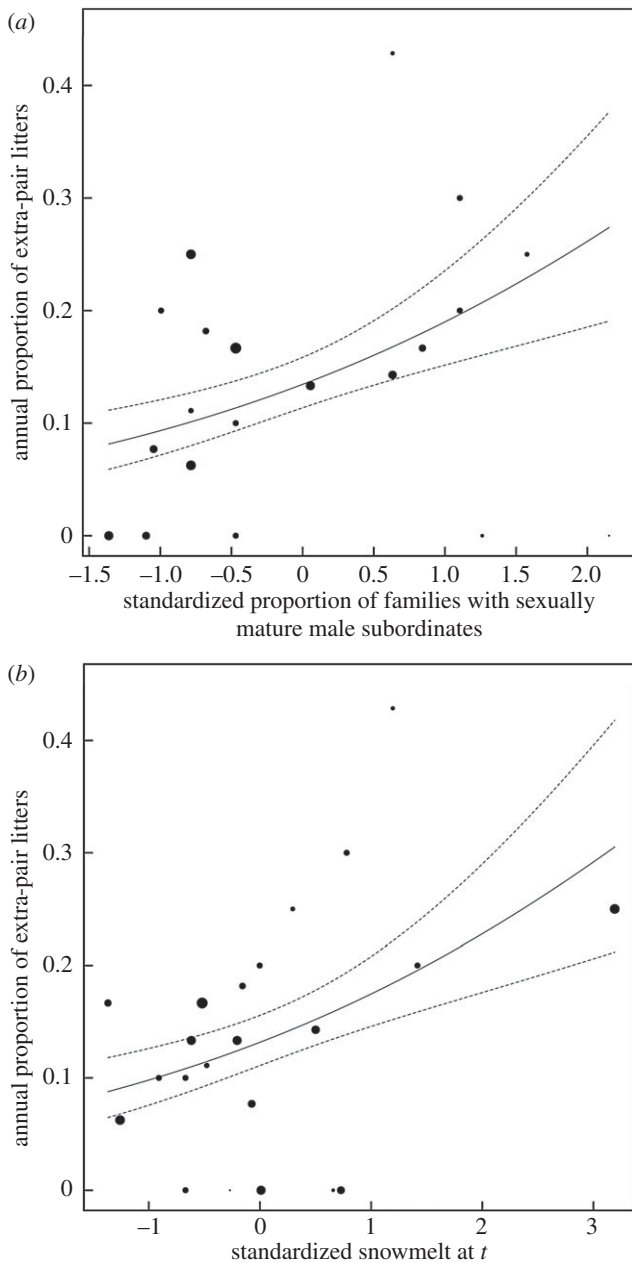


Figure 2. Effects of the population social structure and snowmelt on the annual proportion of Alpine marmots extra-pair litters at La Grande Sassi re (French Alps) between 1992 and 2013. Dots represent residuals of the annual proportion of extra-pair litters after accounting for the effect of the standardized snowmelt at t (a), and residuals of the annual proportion of extra-pair litters after accounting for the effect of the proportion of families with sexually mature male subordinates (b). Dot size is proportional to the number of litters. Lines represent the model predictions (bold) and their associated standard errors (dashed).

the annual variations of the proportion of EPLs (details in electronic supplementary material, appendix S4).

4. Discussion

Over the 22 years of our survey, the annual proportion of EPLs in this Alpine marmot population depended on climatic conditions. It directly increased with early springs and indirectly with snowier winters that resulted in a higher proportion of families with sexually mature male subordinates, a social context favouring EPP [26]. Climatic conditions are thus a key factor to explain the annual proportion of EPLs in Alpine marmots.

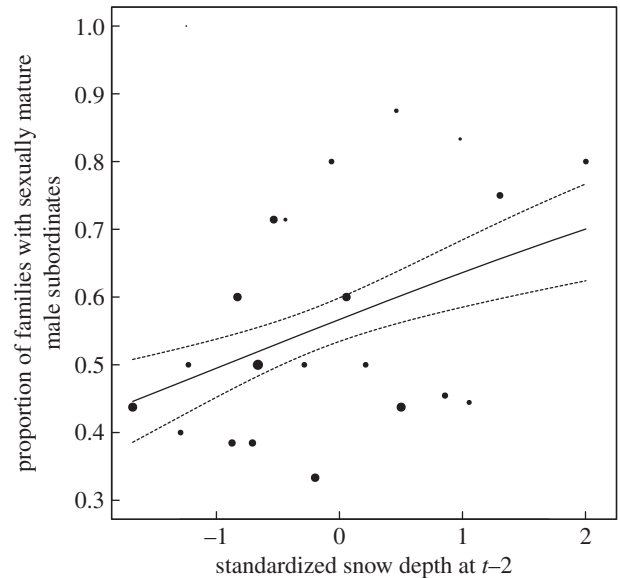


Figure 3. Effects of snow depth 2 years before on the proportion of families with sexually mature male subordinates of Alpine marmots at La Grande Sassi re (French Alps) between 1992 and 2013. Dots represent the proportion of families with sexually mature male subordinates as a function of the standardized snow depth at $t-2$. Dot size is proportional to the number of families. Lines represent the model prediction (bold) and its associated standard errors (dashed).

An earlier snowmelt is associated with a higher proportion of EPLs in Alpine marmots, while the amount of snow in winter is not. Relaxed energetic, movement and time constraints on extra-pair matings are likely to explain this pattern. A lower snow depth during hibernation lowers the body mass of females, right after emergence from hibernation in the same population [27]. But, early snowmelt allows for rapid compensation of the higher energy loss when the snow layer is thin [38]. Despite unfavourable winter conditions, earlier springs are thus likely to result in more energy to allocate to extra-pair matings in Alpine marmots. This is in agreement with a trade-off between extra-pair mating behaviour and self-maintenance [39], whereby good environmental conditions alone would enable enough food intake for energy to be allocated toward extra-pair matings [40,41].

An earlier snowmelt can further allow female and especially male marmots to be more mobile in search for extra-pair mates, in line with the hypothesis that good environmental conditions facilitate movements to find extra-pair mates [42]. Climate is indeed well known to affect animal movement, altering both its range and timing and this, under a wide variety of contexts, range from seasonal migration to natal and breeding dispersal [43,44]. By strongly increasing the energetic demand linked to locomotion [45,46], snow depth strongly limits animal mobility [47]. Thus, the timing of snowmelt is likely a major constraint affecting the probability to encounter mates for species living in snowy environments.

Finally, good environmental conditions are expected to lead to a longer mating season and thus, to more time to find extra-pair mates [11]. A study conducted in 2000 showed that yellow-bellied marmots emerged from hibernation earlier than they did 23 years before, due to climate change [48]. Although the date of emergence from hibernation is unknown in our studied population, Alpine marmots are also very likely to emerge earlier when snow melts earlier and the mating season is likely to be extended. Indeed, in our

population, a trend for pups to emerge earlier from natal burrows has been observed (4.19 days between 1992 and 2013, electronic supplementary material, appendix S2), particularly when snowmelt is earlier (electronic supplementary material, appendix S2). This pattern may probably be extended to other hibernating rodents.

A critical negative impact of spring snow cover on multiple mating has also been reported in other hibernating rodents. In the eastern chipmunk (*Tamias striatus*), multiple paternities increase from 25%, when mating occurs in spring (a mating season characterized by cold temperature, deep snow cover and very low activity), to 100%, when mating occurs in summer [12]. Similarly, in the yellow-bellied marmot, multiple paternities are rare when the snow layer at emergence is deep, when the emergence date is late, and when females are thin [16]. For the yellow-bellied and the Alpine marmot, energetic, movement and time constraints linked to snow cover are likely to cause the observed pattern in these two closely related species [12,16].

A snowy winter has an indirect effect on the proportion of EPLs via a delayed increase of the proportion of families with mature male subordinates 2 years later while it does not directly affect the proportion of EPLs the very same year. A high snow depth ensures burrow insulation during hibernation, leading to larger litters [27] and favouring pup survival [28]. In turn, it results in more families with mature male subordinates 2 years later. The presence of numerous male subordinates limits the capacity of the dominant male to control its female and its competitors (both inside and outside of the group), thus favouring female extra-pair mating opportunities [26]. EPP occurrence is higher among group-living than pair-living species [19,49] and positively correlated with group size and breeding density within species [50–52]. Climate, through its influence on reproduction and survival [53,54], is likely to modify the social structure of numerous mammalian species [55,56]. For instance, in Kalahari meerkats (*Suricata suricatta*) [57], rainy years increase subordinates' emigration and dominants' reproduction, modifying the age structure of social groups. Although the impact of climate change on demographic parameters such as reproduction and survival are now widely accepted [6,53,54,58,59], the indirect repercussions of such climatic effects on mating tactics are still largely neglected despite being very likely to affect the mating system of a wide range of species.

Although most studies so far have focused on inter-individual variability in extra-pair mating behaviour [10,11], ecological factors, and especially climatic conditions, are likely to affect the variability of such behaviour at higher levels of organization: between species [9], between populations [60] or between years (as demonstrated in this study). While neglected, annual behavioural changes could

have profound implications on the genetic characteristics of the population. Indeed, females generally engage in extra-pair copulations to obtain genetic benefits for their offspring and, as a consequence, improve their fitness [61]. In sand lizards, the mean number of fathers per clutch is higher in warmer years [14], and offspring from multiple sired clutches present less malformations and show enhanced first year survival [14,62]. By constraining EPP opportunities at the annual level, climate conditions are likely to shape the genetic characteristics of the population and its annual variability through both changes in female mate choice and effective population size and could have profound implications on the direction and strength of sexual selection. This structuring effect could further have a drastically different outcome regarding the demography of the population. Therefore, climatic conditions are likely to modify population viability and species persistence.

Here, we highlight that climate can affect mating systems through complex pathways. In a context of rapid climate change and increased climatic unpredictability, whether individuals will have the capacity to conduct appropriate mate choice, and thus to produce adapted progeny is a major issue. Yearly modifications of mate choice and extra-pair mate choice are indeed particularly important for next-generation adaptive genetic diversity and we will need to understand these pathways, as well as their repercussions at different levels of organization, to predict the evolutionary impact of climate change.

Ethics. The fieldwork conducted was undertaken after deliverance of the permit number AP n82010/121 by the Préfecture de la Savoie. A.C. is authorized for experimentation with animals (diploma n8R45GRE-TAF110). The protocol has been approved by the ethical committee of the University of Claude Bernard Lyon 1 (n8BH2012-92 V1).

Data accessibility. Data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.n59d1> [63].

Authors' contributions. A.C. and D.A. designed the study and collected the field data. C.B. and S.S. performed the genetic analyses. A.C. and C.B. performed the statistical analyses. All authors co-wrote the manuscript.

Competing interests. We have no competing interests.

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