

# Various responses of pine marten morphology and demography to temporal climate changes and primary productivity

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## Research Article

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## Abstract

Climate and environmental changes affect species' morphology and ecology; however, the response of a species to changes in abiotic and biotic factors is not always consistent. Here, we tested how the structural body size of the pine marten and its population sex ratio changed over time and alongside climate change. We analysed temporal changes in morphological traits using 11 measurements of pine marten skulls collected between 1903 to 2020, linking them with climatic and primary production variations. We assessed demographic changes by calculating temporal sex ratio changes over 61 years. Skull size, as a proxy of body size, increased in response to warmer and less snowy winters, with a three-year time-lag. However, changes in primary productivity rapidly shaped postorbital constriction regardless of body size changes and without time-lags, potentially demonstrating increased diet diversity in pine marten. According to climate change, the population sex ratio has skewed towards males over time. Our results suggest that climate conditions and primary production affect skull structural size, highlighting the potential various responses of pine marten morphology and ecology in relation to climate change. Recently changing population demographics, as a consequence of these processes, may constitute a threat to marten populations.

## Introduction

Climate change is a multi-variable phenomenon that can impact species' distribution, phenology, body size, and condition (Elmhagen et al. 2015; Laidre et al. 2020; McLean and Guralnick 2021). Species' responses to climate change may have a cascading effect on population density and demography, and thus affect interactions between species in the community by altering competition or predation (Lancaster et al. 2017). Some species and population responses are well documented and projected by ecological theories or ecogeographic rules (Tian and Benton 2020). For example, in line with Bergmann's rule, endotherms are larger in higher latitudes and colder climates (Bergmann 1847; Blackburn et al. 1999). By contrast, the body size of these animals decreases in response to climate change, assuming that both spatial and temporal responses to climate conditions are driven by the same factor, e.g., heat conservation (Mayr 1956). The shrinking of body size has been proposed as the third ecological response to recent climate change (Sheridan and Bickford 2011). However, some species have evidenced a significant tendency that directly opposes Bergmann's rule (smaller body size in low-temperature areas; Riemer et al. 2018); in these species, an increase in body size should be expected with warming temperatures. Thus, the response of body size to temporal and spatial climate variation depends on taxa and ecological guilds (Gardner et al. 2011) and is likely related to the different adaptations of animals to avoid heat stress.

Climate change has promoted increases in primary production, especially in mid- and high latitudes, by easing multiple climatic constraints to plant growth (Nemani et al. 2003). Over time, this may cause body size increase in line with the resource availability hypothesis (Geist 1987; Rosenzweig 1968). This prediction was confirmed by the observation that berry shrub abundance increases as a result of warming temperatures (Svensson et al. 2018). Berry crops are major predictors of the summer populations growth of rodents (*Myodes* and *Peromyscus*), which in turn contributes to the increase in the abundance and body size of predators hunting those rodents (Yom-Tov 2008; Krebs et al. 2019). Changes in food availability induced by climate change may also improve animals' body condition (Laidre et al. 2020) and this may affect the sex structure (Cameron 2004). According to the Trivers–Willard hypothesis, in polygynous and sexually dimorphic mammals, females in good condition would achieve higher fitness by producing more male offspring (Trivers and Willard 1973). Therefore, increasing habitat productivity may skew the litter sex ratio towards males. Furthermore, among species demonstrating high sexual dimorphism, food availability may constitute a crucial determinant of survival for both offspring and adult members of the larger sex. As larger males need more food to satisfy their energy requirements, increasing food availability would have a more positive effect on their survival (Peeters et al. 2017; Qu et al. 2016). Considering these findings, increased food availability should cause an increase in body size and a greater contribution of the larger sex to the population.

The analysis of the impact of climate change and habitat productivity on body size or sex ratio requires an extensive time series of measurements (ideally covering the last 100 years). Specimens from zoological collections provide an opportunity to study the temporal variations of both body size and sex ratio (Gower et al. 2019). Additionally, skull size is a good predictor of overall body size (Johnson 1991). Temporal changes in both ambient temperature and primary productivity may, however, have a different influence on various skull measurements as skull dimensions are a composite trait, which is associated with a large suite of diverse functions. Some skull components are strongly correlated with body mass (e.g. skull length) and are thus probably related to temperature variation, while others are a result of diet composition (e.g. skull structures related to chewing and biting force; Haba et al. 2008) and may be related to primary productivity which affects the availability of various food types. Therefore, temporal changes in the size of

different parts of the skull provide an opportunity to study the morphological and behavioural (food habits) responses of animals to climate and primary productivity changes, which are not necessarily changing at the same velocity.

Some marten species, such as the pine marten (*Martes martes*), the American marten (*M. americana*), and the stone marten (*M. foina*), present a trend in body size changes that contradicts Bergmann's rule (Reig 1992; Riemer et al. 2018). Pine marten, a medium-sized carnivore with apparent sexual dimorphism (Reig and Ruprecht 1989), is smaller in the colder climates of north-eastern Europe and larger in the warmer climates of south-western Europe (Meiri and Dayan 2003; Monakhov and Hamilton 2020; Reig 1992). The mechanisms of this phenomenon have not been well explained; nevertheless, it is likely that smaller individuals benefit more from behavioural thermoregulation, as they need less energy when reducing activity and spending the coldest days in warm microsites. As a result, studying the temporal variability in the size of the pine marten skull can provide additional insights into how animals adapt to different environmental conditions and their response to condition changes. In addition, pine martens inhabit various forest types in their European range (Brainerd and Rolstad 2002; Wereszczuk and Zalewski 2015). Forest habitats in some large complexes vary only slightly with time, such as the Białowieża Forest (Samojlik et al. 2013); therefore, changes in habitat structure may only have a minor impact on body size and demographic structure. Recent research has demonstrated an increase in pine marten body weight in accordance with warming temperatures in the last 60 years (Wereszczuk et al., in press). These changes can be related either to increased structural body size or to increased body condition or both.

The aim of the present study was to examine how the structural body size of the pine marten (independent from body condition) and population sex ratio has changed over the last 117 years. To investigate this, we analysed the morphology of crania and mandible variation in relation to the temporal changes of multiple climate and environmental variables. We tested the following hypotheses: (1) as the pine marten showed a trend that opposes Bergmann's rule, their body size increases over time due to increases in temperature; (2) according to the resource availability hypothesis, body size increases with a temporal increase in primary productivity; (3) temperature and primary productivity variations over time affect parts of the skull in relation to their function; and (4) the proportion of males in the population increases over time.

## Material And Methods

### Data collection

We measured 158 pine marten skulls collected between 1903 and 2020 originating from two sites: (1) The Białowieża Forest (NE Poland and W Belarus; N=93) and (2) Silesia (SW Poland; N=65; Fig. S1). The Białowieża Forest is the best-preserved forest area in the European lowland (Jaroszewicz et al., 2019), while Silesia includes Bory Dolnośląskie, which is one of the largest complexes of forests in Europe. The specimens were collected in the Museum für Naturkunde Berlin, the Zoological Institute of the Russian Academy of Sciences in Saint Petersburg, the Museum of Natural History, Wrocław University, and the Zoological Collection of the Mammal Research Institute Polish Academy of Sciences (MRI PAS). For each skull, measurements of 11 traits were made with an electronic calliper (with an accuracy of up to 0.01 mm): condylobasal length, maxillary tooth-row length, palatal length, zygomatic width, interorbital constriction width, postorbital constriction width, mastoid width, mandibular tooth-row length, mandible height, mandible length, and braincase height, as per Reig and Ruprecht (1989) (Fig. 1). All measurements were carried out by one observer in order to avoid measurement errors. We excluded young individuals with incomplete fusion of the cranium bones and juvenile teeth.

To analyse temporal sex ratio changes, in addition to the data set used for skull measurements, we also used data from sexed individuals, mostly roadkill, collected in the MRI PAS, whose skulls were damaged or not collected, which increased the dataset to 205 individuals (72 females and 133 males) between the years 1959 and 2020. The probability of being male was analysed for the last 61 years because of the collected data was more evenly distributed over the years analysed without large time gaps.

### Climate data

We obtained monthly temperature (temp), precipitation (prec) and snow cover (snow) and averaged them for the winter period (from November of the previous year to February of the skull collection year; tempWINT, snowWINT) and/or summer (May–August of the skull collection year; tempSUMM, precSUMM) for each study site separately. We also used average carbon mass flux from the atmosphere due to Net Primary Production (NPP) in the months of peak vegetation, representative for Europe (May–August;

nppSUMM; Hicke et al., 2002), to assess intensity of the influence of NPP on skull variation. Climate data were obtained from the Land Surface, Snow and Soil Moisture Model Intercomparison Project (LS3MIP; van den Hurk et al., 2016) developed under the sixth phase of the Coupled Model Intercomparison Project (CMIP6; Eyring et al., 2016). To obtain variables from across the entire study period, we used two LS3MIP models: Land-Hist and LFMIP-rmLC. The Land-Hist historical simulation covers the period 1850 to 2015 and provides a comprehensive assessment of land surface, snow and soil moisture–climate feedbacks. The LFMIP-rmLC model was designed to simulate the impact of a future climate on land surface and was extended to 2100 (van den Hurk et al., 2016). To cover the study period 1900–2020, we obtained climatic variables from Land-Hist from 1900 to 1970 and from LFMIP-rmLC from 1971 to 2020. Both data sets are highly correlated in the overlapping period of 1970–2015 ( $r = 0.93$ ,  $p < 0.001$ ); therefore, it was possible to combine them into one data set.

## Statistical analysis

All analyses were conducted in R version 4.0.3 (R Core Team, 2020). We tested body size variation predicted by crania and mandible variables across a long-term trend (117 years), using a generalized additive model (GAM; package 'mgcv' version 1.8; Wood, 2017). To reduce the number of variables for skull measurements entering the model, which are often highly correlated, we performed a principal component analysis (PCA) of skull measurements using the PCA function ('FactoMineR' package; Lê 2008). Due to damage to some skulls and missing measurements (depending on the type of measurement, damage was from 4% to 17%), we conducted a PCA based on an estimated covariance matrix obtained by function `imputePCA` ('missMDA' package) which uses regularised iterative PCA to impute and estimate the covariance matrix of incomplete data (Josse and Husson, 2016; Nassiri et al., 2018). The GAMs were conducted separately for condylobasal length, first principal component (PC1), and postorbital constriction width, with year, sex, and site (two-level factor: Białowieża Forest and Silesia) as explanatory variables. We added sex and site as explanatory variables to control the effects of sexual dimorphism and differences in marten size between sites. We used condylobasal length separately, as this measurement is most often used to predict body size, to which it is highly correlated (Ochocinska and Taylor, 2003; Yom-Tov et al., 2003), and postorbital constriction width, which reflect chewing and biting force, as only this measurement was not correlated with PC1 (see Results). Isotropic thin plate regression splines with knot-based approximations were used for temporal smoothing. Models were specified using Gaussian distribution, an identity link function, and an REML approach.

In the next step, we tested crania and mandible variation in relation to climatic condition and primary productivity using four climatic variables and one primary productivity variable: `tempWINT`, `tempSUMM`, `snowWINT`, `precSUMM`, and `nppSUMM`. We were not able to obtain data about the years of birth of the martens, only their year of death. Pine martens can survive up to 11 years with an average lifespan of 3 years (Marchesi, 1989); therefore, climatic variables in the year of death do not represent the conditions during life, which most affect skull size (Geist, 1987; Searcy et al., 2004). In order to explain the effect of temporal changes in climate and NPP on body size, we used GAM-predicted climatic variable values by year as proxies of temporal changes of those variables (Fig. 2). Thus, we obtained smoothed values for each climatic variables and NPP corresponding to the annual temporal trend of each variable separately for each site (Fig. 2).

To test the influence of climatic conditions and NPP on skull size, we first used a GAM (as previously) but the relations were linear. Consequently, we used a linear model (LM) with climatic, NPP, sex, and site as explanatory variables. Variance inflation factors (VIFs) indicated collinearity among all climatic explanatory variables (Table S1); thus, models were conducted separately for each climatic and NPP explanatory variable. A set of five LM models, each with one relevant climatic or NPP variable, were performed for condylobasal length, PC1, and postorbital constriction width and their performance compared by Akaike information criterion (AIC) values. Models within  $\Delta AIC < 2$  were assumed to be equally parsimonious (Harrison et al., 2018). To account for climatic conditions during body growth, the influence of predicted climatic variable values on condylobasal length, PC1 and postorbital constriction width were considered with different time-lags ( $\text{year}_t$ ,  $\text{year}_{t-1}$ ,  $\text{year}_{t-2}$ ,  $\text{year}_{t-3}$ ) using LM and then compared by their AIC values.

Temporal trends in sex ratio were examined using logistic regression (GLM with binomial error distribution and logit link), with sex as the dependent variable and year and site (two-levels factor: Białowieża Forest or Silesia) as explanatory variables. We tested whether the probability that a collected individual would be a male (1) or a female (0) was predicted by time. Next, we tested probability of being male in relation to climatic and NPP variables, building five GLMs with sex as the dependent variable and site and one of the climatic or NPP variables as explanatory variables and then comparing by AIC values of those models.

## Results

We measured the condylobasal length of 138 skulls, the postorbital constriction width of 137 skulls, and PCA was performed for all (158) skulls. The PC1 explained 90.5% of the total morphological variance and could be used as an integral measure of skull size in the pine marten (Table S2). All traits were included in PC1, with factor loadings greater than 0.93, with the exception of postorbital constriction width. The second principal component (PC2) contained only postorbital constriction width with a factor loading of 0.81.

Body size, as predicted by the response variables of condylobasal length and PC1, differed between sexes and sites – males and individuals from Silesia were significantly larger than females and individuals from the Białowieża Forest (Table 1). Over the past 117 years, the body size of the pine marten was stable between 1903 and 1960 and increased considerably from 1960 onwards (Fig. 3). Postorbital constriction width, reflecting chewing and biting force, was greater in individuals from Silesia and in males, and it fluctuated non-linearly over the years (Table 1).

Table 1

Results of GAM analyses of the sex, site, and smoothed effect of year-related skull morphometry of the pine marten between 1903 to 2020. CBL – condylobasal length of the skull; PC1 – the first principal component representing integral measure of skull size in the pine marten; postorbital constriction width represented the second principal component.

Variables	CBL				PC1				Postorbital constriction width			
<i>Parametric terms:</i>												
	Estimate	SE	t	p	Estimate	SE	t	p	Estimate	SE	t	p
Intercept	77.12	0.25	309.92	<0.001	-4.15	0.19	-21.77	<0.001	17.96	0.19	96.27	<0.001
Sex (male)	6.84	0.29	23.93	<0.001	5.64	0.21	26.23	<0.001	0.54	0.22	2.52	0.01
Site (Silesia)	0.81	0.28	2.87	0.0048	1.34	0.21	6.44	<0.001	0.90	0.21	4.24	<0.001
<i>Smooth terms:</i>												
	EDF max	EDF	F	p	EDF max	EDF	F	p	EDF max	EDF	F	p
s(year)	2.15	2.56	4.08	0.0095	2.38	2.84	6.29	<0.001	4.68	5.69	2.27	0.03

In all five univariate models analysed, condylobasal length and PC1 variations in relation to climate and NPP changes – three for condylobasal length and two for PC1 – were more parsimonious, as measured by AIC ( $\Delta AIC < 2$ ; Table 2). Snow cover in winter and average winter temperature best explained skull size changes for both condylobasal length and PC1; additionally, average summer temperature explained condylobasal length changes, while summer precipitation and NPP revealed no significant effect on skull size (Table 2; Table S3). Pine marten skull size increased with commensurate increases in winter and summer temperatures and with decreases in snow cover depth over time (Fig. 3). Conversely, only one parsimonious model was selected for postorbital constriction width (compared to their performance with AIC), which was positively correlated with NPP.

Table 2

Results of linear model selection for skull morphometry of pine marten (N=158), condylobasal length (CBL), PC1, and postorbital constriction width in relation to climatic variables and primary productivity between 1903 and 2020. Models ranked by Akaike's information criterion scores ( $\Delta\text{AIC}$ ) for candidate climatic models. Top-ranked models are in bold ( $\Delta\text{AIC} < 2$ ).

Climatic variables	CBL			PC1			Postorbital constriction width		
	AICc	$\Delta\text{AIC}$	$\omega_i$	AICc	$\Delta\text{AIC}$	$\omega_i$	AICc	$\Delta\text{AIC}$	$\omega_i$
snowWINT	531.45	<b>0.00</b>	0.43	535.40	<b>0.00</b>	0.48	461.0	4.00	0.09
tempWINT	532.18	<b>0.73</b>	0.30	536.35	<b>0.95</b>	0.30	461.09	4.09	0.08
tempSUMM	533.30	<b>1.85</b>	0.17	538.02	2.63	0.13	461.21	4.21	0.08
precSUMM	534.60	3.15	0.09	538.79	3.39	0.09	460.89	3.89	0.65
nppSUMM	540.29	8.84	0.01	548.28	12.88	0.00	<b>457.0</b>	<b>0.00</b>	<b>0.65</b>
snowWINT – average winter snow cover depth; tempWINT – average winter temperature; tempSUMM – average summer temperature; precSUMM – average summer precipitation; nppSUMM – average summer Net Primary Production.									
AICc – Akaike's information criterion with a second order correction for small sample sizes; $\Delta\text{AIC}$ – difference in AICc between a given model and the most parsimonious model; $\omega_i$ – weight of the model.									

A comparison of time-lags within each climatic variable indicated that the climatic variables of the three years prior (year  $t-3$ ) best explained variability in skull size (condylobasal length and PC1; Table S4), while postorbital constriction width was best explained by NPP in the year the animal was obtained (year; Table S4). However, time-lags only slightly improved the model.

Sex ratio was male-biased and the proportion of males increased over the years from 0.53 in 1959 to 0.73 in 2020 ( $t = 0.015$ ,  $p = 0.018$ ; Fig. 4). Site had no significant effect on the sex ratio ( $t = -0.07$ ,  $p = 0.825$ ). Among the five univariate models testing the proportion of males in relation to climatic and NPP variables, four were more parsimonious as measured by AIC (Table S5). A male sex bias was observed with increases in winter and summer temperature and decrease of summer precipitation and snow cover depth.

## Discussion

Our results suggest stable skull size in the pine marten between 1900 and 1960 and increasing skull size since 1960, when climatic variables began to change rapidly over time. In general, skull size, and by implication body size, was strongly correlated with variations in climatic conditions: increasing winter temperature and decreasing snow cover positively affect the body size of the pine marten. The average body size in a population in a given year is mainly related to (1) the growth rate during the first six months of life and (2) the survival of individuals of various body size through extreme periods. Increasing winter temperatures may influence the survival of larger individual pine martens. In response to low temperatures, pine martens limit their activity and daily movement during harsh winter days and select well-insulated microsites during the day to optimise their energy budget and avoid heat loss (behavioural thermoregulation; Zalewski 2000; Zalewski et al. 2004). Selected microsites have a substantially warmer temperature than the ambient air temperature outside (Buskirk et al. 1988). As a result, declines in marten activity during the winter result in energy saving by both reducing the time spent in energy intensive activities, such as locomotion, and by increasing the time spent within an insulated environment when outside temperature are relatively low. Some physiological features of martens further enhance their energy conservation during this resting time. Martens lower their body temperature by 2.9°C on average while at rest (Buskirk et al. 1989). Therefore, the increase in resting periods is highly important in energy conservation. With low activity and short daily distances travelled, martens, similarly to other mustelids that curtail their activity on colder days, have difficulty finding sufficient food to satisfy their energy needs (Gilbert et al. 2009; Zub et al. 2011). Another behavioural strategy that allows martens to reduce their activity is food caching. Pine martens often hide large prey items, such as squirrels, hare, and grouse, in their resting sites and use them during days of low activity (Grakov 1970; Pulliainen 1981). In the coldest winter months, pine martens eat more squirrels and the carcasses of deer and wild boar (Zalewski 2000). However, the hidden food can allow smaller individuals to survive the lowest temperatures for longer than larger individuals. A model based on time–energy budgets for weasel-like mustelids predicts that small individuals need less energy during the period of activity limitation in comparison to bigger individuals (Zub et al. 2011). Therefore, large individuals potentially reduce their activity for shorter periods and they are forced to be active during days of low

ambient temperature. This may potentially decrease the survival of large individuals on days with very low temperature. Consequently, decreasing winter severity should result in greater winter survival of larger individuals and an increasing proportion of those individuals in the population.

We observed an increase of pine marten body size with decreasing snow cover over time. High snow cover impedes movement and limits hunting success, resulting in decreased rodent consumption in years with high snow cover (Jędrzejewski et al. 1993). Therefore, a decline in snow cover increases the hunting success of martens concerning rodents (Jędrzejewski et al. 1993). Higher hunting success reduces the need for longer daily movement distance and exposure to low ambient temperatures (Zalewski et al. 2004). The influence of snow cover on marten body size also confirms the slight decrease in condylobasal length and PC1 observed in the period 1900–1940, likely caused by increases in snow cover in that period (compare Figs. 2 and 3). It thus seems likely that decreasing snow cover promotes the acquisition of more energetic food, which allows the survival of larger individuals.

A three-year time-lag in skull size change in response to climatic variability may suggest that climatic conditions during the growth period (three years earlier) determine the body size of an adult individual. The adult body size results from the length of time when high-quality food is consumed during growth (Desy and Batzli 1989; Geist 1987). Climate change may cause increased food abundance during this period as it drives primary production in mid and high latitudes (Nemani et al. 2003), causing a cascading effect as a result of higher seed and fruit production (Bogdziewicz et al. 2020; Svensson et al. 2018) and leading to increased numbers of rodents (Czeszczewik et al. 2020; Krebs et al. 2019), the main prey of pine martens (Jędrzejewski et al. 1993). Pine marten diet composition follows changes in rodent numbers and the consumption of rodents by martens has increased over the last four decades (Drwęcka 2021; Jędrzejewski et al. 1993). A higher availability of high-quality food items may satisfy the increased nutritional demands of growing individuals during the first six months of life.

Overall, both explanations – an increase in the survival of large individuals due to warming temperatures and an increase in the growth rate during the first six months of life related to increased food abundance – are not mutually exclusive. An increase in rodent abundance causes an increased rate of growth in juvenile animals and a relaxation in thermal stress with warming temperatures facilitating the survival of larger individuals into the spring. Accordingly, winter survival related to body size would shape the average body size in the marten population, but higher food abundance allows growth to larger body sizes which are then subject to selection by the following winter conditions. The high correlation of marten body size with winter temperature and snow cover may support this scenario. However, our current understanding of the influence of climate change–primary productivity–food abundance is limited. Based on our results, we speculate that a body mass increase driven by rising productivity should be preceded by an improvement in body condition. The body size changes induced by the higher rate of winter survival of larger individuals should influence the age structure within the group of larger individuals over time.

In contrast to all other skull morphological measurements, postorbital constriction width followed NPP changes, independent of changes in skull size over time and without time-lags. NPP changes may provide greater availability of various food sources, which may cause the pine marten to expand its diet resulting in changes in skull shape. Increasing NPP may expand dietary breadth with increased richness and availability of food resources, as has been shown for large carnivores (Ferretti et al. 2020). Relatively narrower postorbital constriction width permits a larger anterior part of the temporalis, which, together with the zygomatico-mandibularis muscle, are responsible for the biting force of the fully open jaw and may indicate an adaptation towards hypercarnivory (Loy et al. 2004; Wiig 1982; Wiig 1986). The width of the postorbital constriction reflected differences in chewing and biting force between two subspecies of Japanese raccoon dog and demonstrated that a greater postorbital constriction width, in addition to the development of premolars and molars, indicates an adaptation to feeding on fruits and insects (Haba et al. 2008). Similarly, an increase in the postorbital constriction width of the pine marten with increased NPP may demonstrate a shift towards a more varied diet. Silesia is characterised by an overall higher NPP than the Białowieża Forest, and pine martens originating from Silesia had a greater postorbital constriction width, indicating a consistency with the temporal pattern of postorbital constriction width increase with NPP. According to Haba's inference (Haba et al. 2008), smaller postorbital constriction width may indicate an adaptation of feeding behaviour to survive the colder environment by focusing on fat-rich foods, such as mammals and birds. In environments with milder climates, the length of fruiting extends and the pine marten often consumes more fruit and fewer rodents as the former is easier and less costly to obtain (Zalewski et al. 2004; Zhou et al. 2011). This trophic diversity is reflected in postorbital constriction width, which narrows from south-western to north-eastern Europe (Reig 1989). Moreover, NPP increase and, potentially, diet improvement, induce an increase in postorbital constriction width without time-lags, which suggests the high

plasticity of feeding habits and the fast response of skull morphology. This change in skull morphology could be a good indicator for the tracking of animal food habit changes on large spatial scales and over evolutionary time.

Our results support the male-biased sex ratio which can potentially be explained by male over-representation in the litter (according to the Trivers–Willard hypothesis) and/or their lower mortality. However, we were unable to confirm that the predominance of males in the population may be the result of habitat productivity increases but rather the potentially higher survival of males (which are larger than females) in milder climates. The potential higher mortality of females should also be considered; for example, due to higher costs during reproduction and kit rearing or lower mortality of males due to mild winter conditions. However, it is not possible to say which is the most likely to appear in pine marten. Undoubtedly, such a trend coincides with climate change effects and changes in temperature, snow cover depth, and precipitation. The lower proportion of males (0.41) in 1872–1878 from Silesia (n = 46; data not included in analysis due to a large time-gap) supported the trend of increasing males over time. Sex ratio drives sex-specific effects on reproductive outcomes and affects population demography. It skews towards males, resulting in a reduction in effective population size (Charlesworth 2009). The number and survival of reproductive females in polygynous mammal species, such as the pine marten, is the most important factor in long-term population persistence (Dalerum et al. 2008). Thus, a male-biased sex ratio increasing over time may constitute a threat to the marten population. However, it is also possible that the female density is stable over time and only the proportion of males increases; if this is the case, the reproductive outcome would not change over time. The influence of a highly male-biased sex ratio on population density should be tested in future studies.

## Conclusions

Our results revealed that with climate warming changes in various biotic and abiotic conditions affect the morphology and behaviour of animals and, as a consequence, their population demography. The increasing body size of martens augments their energy demands. Therefore, marten predation pressure may increase over time, affecting prey populations. The adaptation of feeding behaviour to environmental changes (widening of feeding habits as suggested by structural changes of skull elements) and a potential reduction in population density (due to male-biased sex ratio) may reduce the pressure on some prey groups. Overall, all this evidence suggests that animal responses to climate change may alter species' interactions within an ecosystem in a complex way.

## Declarations

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### Conflict of interest

The authors declare that they have no conflict of interest.

### Ethics approval

Not applicable

### Consent to participate

Not applicable

### Consent for publication

Not applicable

### Data availability

The data that support the findings of this study are openly available in openforestdata.pl at <https://doi.org/10.48370/OFD/B8AIWI>.

### Code availability

Not applicable

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## Supplementary Information

**Figure S1.** The distribution of the samples in years used to analyse the temporal changes in the skull size and in sex ratio of the pine marten (*Martes martes*) in two study sites. Samples with measured skulls were used only for the analysis of changes in skull size; samples without measurements, together with samples with measured skulls, were used for the analysis of the sex ratio.

**Table S1.** Variance inflation factors (VIFs) for particular explanatory variables used in the analysis of the relationship between the skull size of the pine marten and climate change.

**Table S2.** PC axis loadings for the first two principal components. Highest loadings for each variable are in bold.

**Table S3.** Results of linear models testing for effects of the sex, site, and climatic variables on pine marten skull morphometry between 1903 and 2020. CBL – condylobasal length of the skull; PC1 – the first principal component representing an integral measure of skull size; postorbital constriction width represented the second principal component. The most parsimonious models ranked by Akaike’s information criterion scores ( $\Delta AIC < 2$ ) are in bold.

**Table S4.** Comparison of linear models relating pine marten skull measurements, condylobasal length (CBL), PC1, and postorbital constriction width to climatic variables with different time-lags.

**Table S5.** Results of generalized linear model selection for the proportion of males in the population of pine marten over the last 60 years (1960-2020). Models ranked by Akaike’s information criterion scores ( $\Delta AIC$ ) for candidate climatic models. Top-ranked models are in bold ( $\Delta AIC < 2$ ).

## Figures

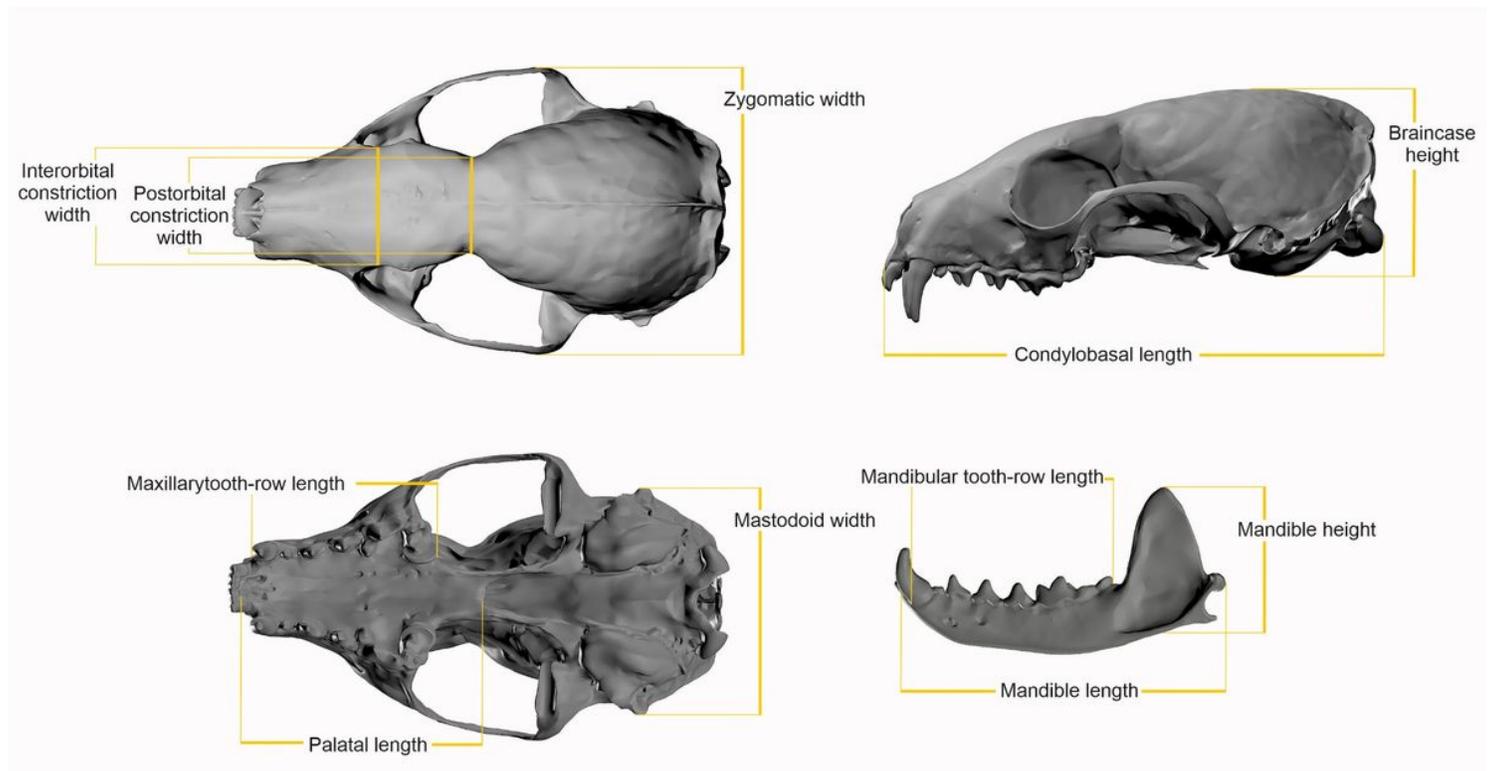
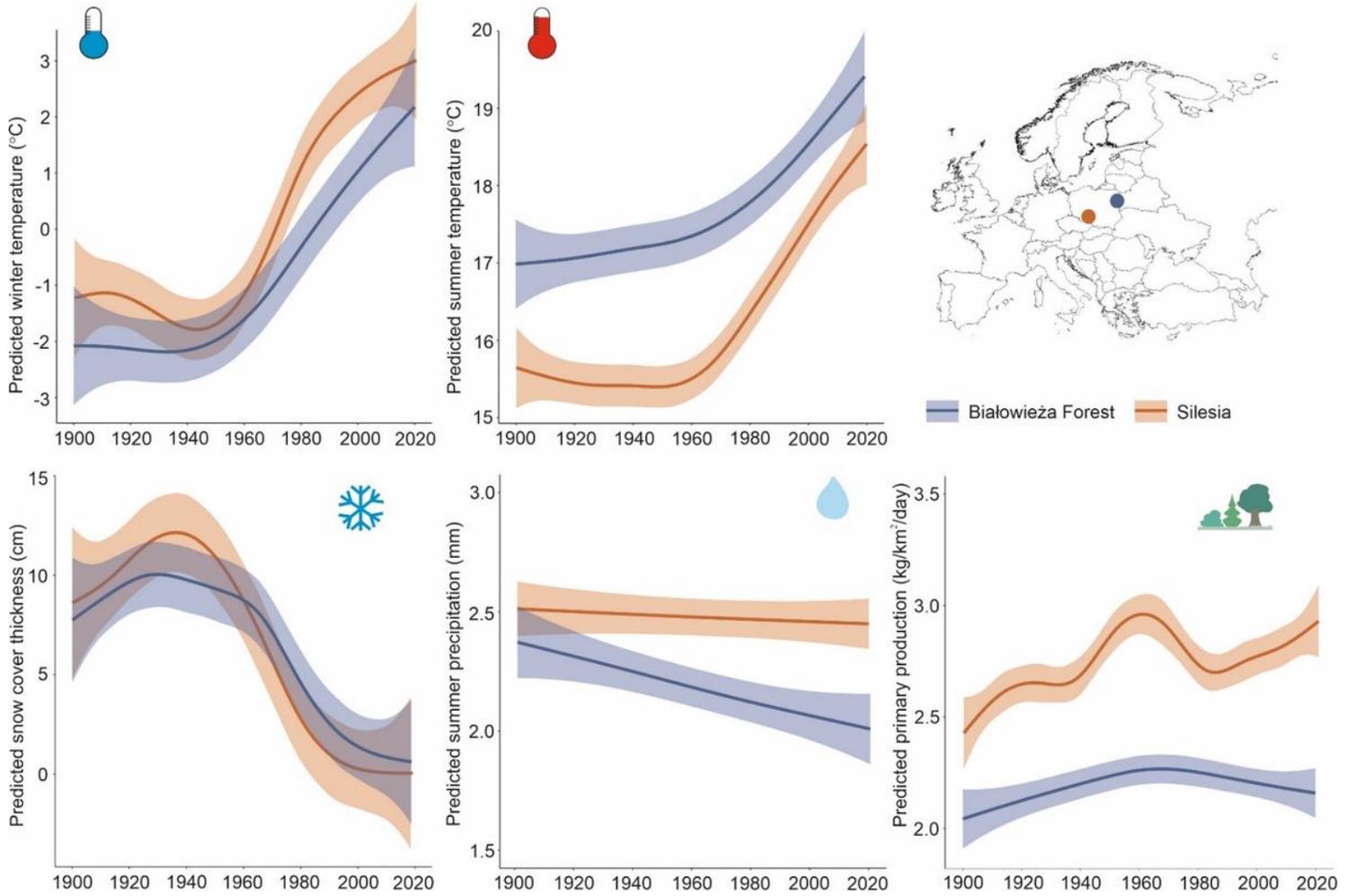


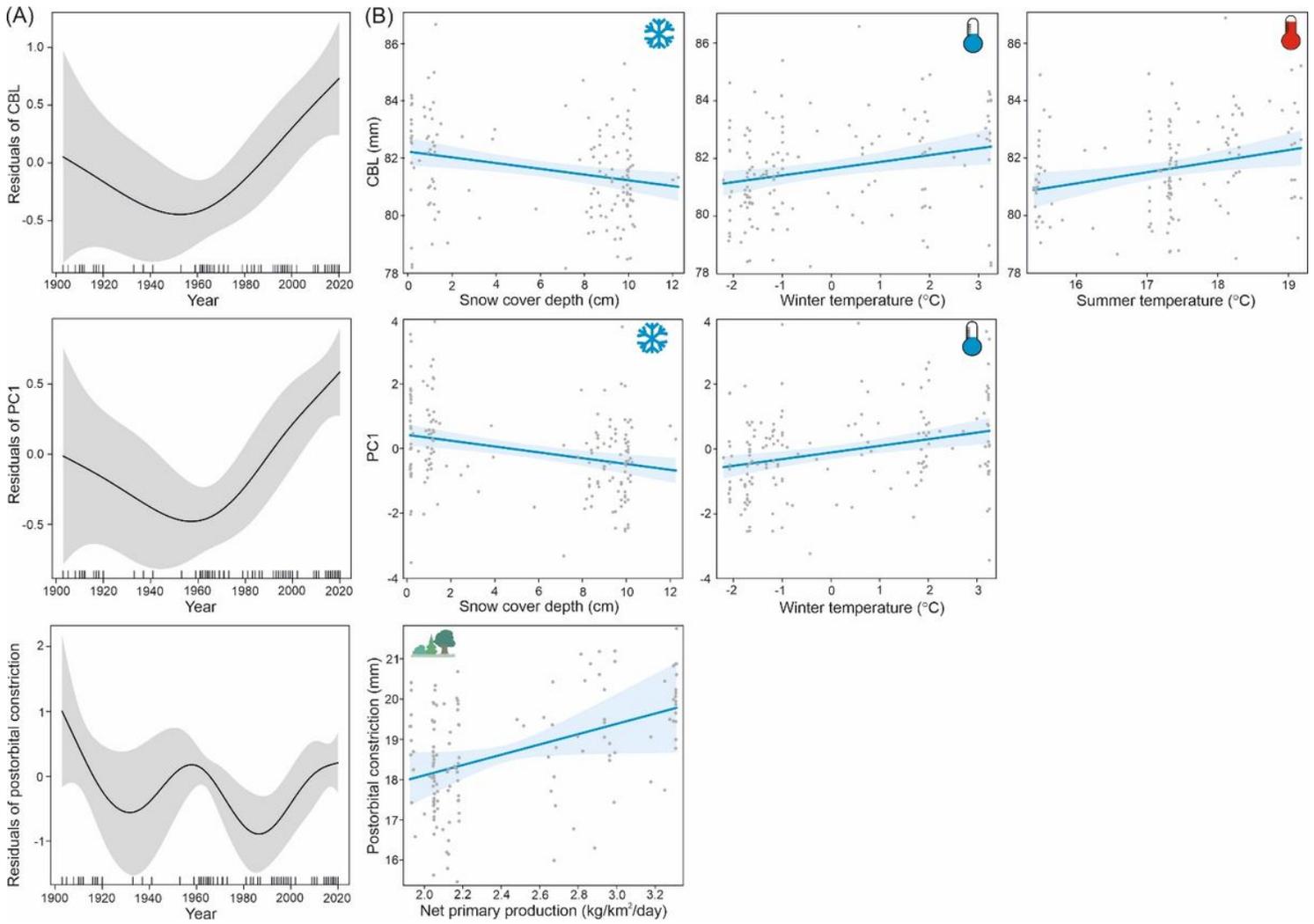
Figure 1

Skull measurements of 11 traits in pine marten. Figure prepared based on 3D scan of specimen *Martes martes* - 31348, Zoological Collection of the Mammal Research Institute, PAS.



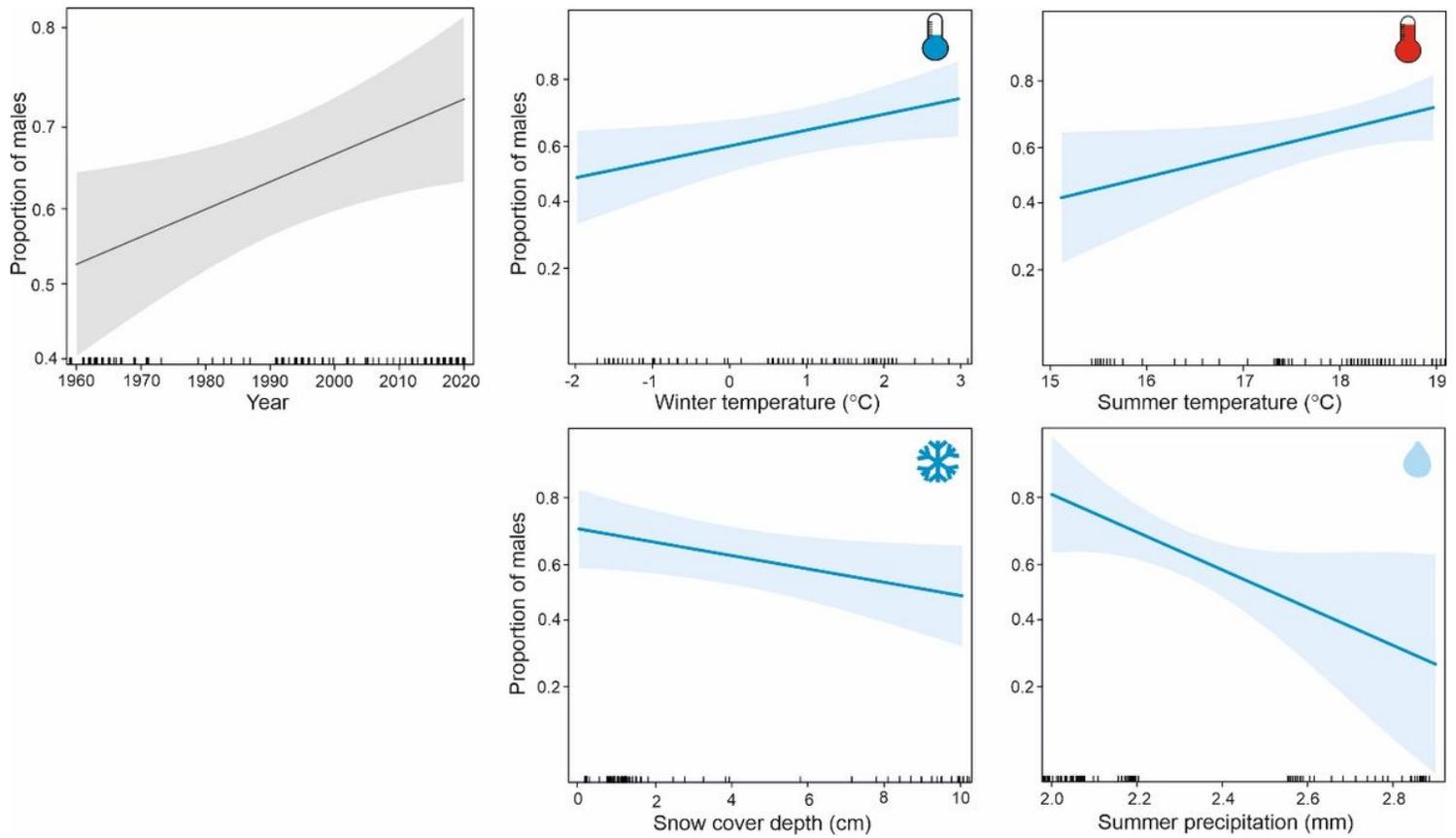
**Figure 2**

Temporal changes of average winter temperature (November–February), summer temperature (May–August), snow cover depth, summer precipitation, and summer Net Primary Production, as predicted by generalized additive models over 120 years in two study sites in Central Europe, based on models from the Land Surface, Snow and Soil Moisture Model Intercomparison Project (CMIP6).



**Figure 3**

Variation in condylobasal length (CBL), the first principal component representing an integral measure of skull size (PC1) and postorbital constriction width of the pine marten collected between 1903 and 2020 as a function of year predicted by generalized additive models (panel A) and as a function of climate and NPP variables predicted by linear models (panel B). Only data with top models ( $\Delta AIC < 2$ ) are presented. The rug plots along the x-axis of panel A show the data distribution. The effects of sex and site not shown.



**Figure 4**

Temporal changes in the sex ratio of the pine marten, expressed as the proportion of males in the population, across two study sites in Central Europe over the last 60 years (1960-2020), predicted by logistic regression. The rug plots along the x-axis illustrate the data distribution. The effects of sex and site not shown.

## Supplementary Files

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