

Weather conditions explain reproductive success and advancement of the breeding season in Western Capercaillie (*Tetrao urogallus*)

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Climate change and associated changes in weather patterns have globally widespread effects on natural systems. Shifts in phenology can affect the reproductive success of birds by causing a mismatch between the onset of breeding and favourable conditions for reproduction, such as a peak in food availability. Weather conditions and their changes have also long been discussed as affecting the reproductive success of grouse (Tetraoninae) and contributing to rapid declines in many central European populations. We monitored the reproductive success of Western Capercaillie *Tetrao urogallus* in the Black Forest, Germany, over a 14-year period to study how weather conditions correlated to reproductive success and to assess whether changing environmental conditions were related to a seasonal shift in reproduction. We observed a temporal shift in peak lekking activity from late to mid-April, which corresponds to an advance of 0.65 days/year. Furthermore, we show that warm conditions during the reproductive season were positively associated with reproductive success (i.e. larger brood size, more hens with chicks and more chicks per hen) and that precipitation volume during the early weeks after hatching was negatively correlated with brood size. Precipitation before copulation (i.e. peak of lekking) affected the proportion of hens with chicks and the number of chicks per hen. Sex ratio in broods was also affected by weather conditions, with more female than male chicks in years with low temperatures and high precipitation. By analysing spring weather predictions for the period 2020–2039, we found that weather conditions during the reproductive period remained constant when assuming a continued advancement of reproduction onset, although annual variation was high. We show the importance of weather conditions in influencing Western Capercaillie reproductive success. Western Capercaillie in the Black Forest seem to adjust the timing of reproduction according to changes in weather conditions, but this advancement is unlikely to be limitless, making the future impact of climate change on the species uncertain.

Keywords: Black Forest, breeding success, climate change, grouse, reproduction, precipitation, temperature.

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The warming of the climate system is causing temporal and spatial changes in weather patterns such as the distribution and frequency of precipitation amounts or extreme weather events (Pachauri

et al. 2014), which have globally widespread effects on natural systems (Walther *et al.* 2002, Pachauri *et al.* 2014). Weather conditions are a major factor in shaping habitats and their suitability for species (Parmesan & Yohe 2003, Parmesan 2006, Chen *et al.* 2011), with changes in weather patterns increasing the extinction risk of geographically restricted populations (Thomas *et al.* 2004, Urban 2015). Although extinction risk does not necessarily correlate with taxonomic group (Urban 2015), among vertebrate species, birds are considered to be particularly vulnerable, because their reproduction typically coincides with seasonal food peaks, and reproductive success therefore depends on appropriate timing (Visser *et al.* 2004, Carey 2009). Changes in weather conditions can therefore cause a mismatch between the seasonal food peaks and the timing of breeding (Carey 2009).

Grouse (Tetraoninae), in particular Black Grouse *Lyrurus tetrix* and Western Capercaillie *Tetrao urogallus* (henceforth 'Capercaillie'), have experienced dramatic declines in abundance and reproductive success in central Europe, most likely due to the effects of large-scale intensification of land-use on habitat suitability (Storch 2007, Ludwig *et al.* 2009, Jähren *et al.* 2016) and associated changes in predator abundance (Kurki *et al.* 2000, Baines *et al.* 2016, Kämmerle *et al.* 2017). Moreover, both changing climate and associated changes in weather patterns have been discussed as potentially contributing factors (Moss *et al.* 2001, Braunisch *et al.* 2013).

Climate and weather conditions affect grouse in different ways. By affecting plant species composition and growth rate, climate is a key factor in the long term in determining the distribution and amount of suitable habitat for grouse, with climate warming expected to reduce the range of the cold-adapted Capercaillie in central Europe (Huntley *et al.* 2007, Braunisch *et al.* 2013, 2014). Weather conditions can directly affect reproductive success in different ways, and cold and wet weather conditions may increase mortality in the precocial chicks as well as their vulnerability to predation (Wegge & Kastdalen 2007, Selås *et al.* 2011, Summers *et al.* 2017). Furthermore, weather conditions drive nutrient availability for European grouse twice a year (Moss *et al.* 2001). First, the availability of new plant growth in late winter and early spring is related to egg quality and chick viability through hen body condition. Secondly, chicks are highly dependent on arthropod availability during

the first weeks after hatching (Klaus *et al.* 1989, Moss 1997, Picozzi *et al.* 1999, Moss *et al.* 2001). The quantities of both food sources can be expected to be largely driven by weather patterns in spring. Due to the sexual dimorphism in the species, weather conditions are also expected to affect the survival of male and female Capercaillie chicks differently. Male chicks may be unable to increase their weight fast enough under wet and cold conditions due to low arthropod abundance and poor conditions for foraging (Klaus *et al.* 1989).

Given increasing temperatures, an advancing onset of the vegetation growth period, and the correlation of local vegetation development and timing of reproduction (e.g. Visser *et al.*, 2004, Carey 2009), climate change may negatively affect the species' reproductive success due to increasing mistiming (Visser *et al.* 2004, Both *et al.* 2006). Whether grouse are capable of compensating for such effects by shifting their reproductive period (Crick & Sparks 1999, Sergio 2003, Liebezeit *et al.* 2014), however, is largely unknown. By contrast, raising temperatures may also have potential benefits, as grouse reproductive success has been positively associated with warm and dry springs (Wegge & Rolstad 2017) and higher temperatures in the days after hatching (Wegge & Rolstad 2011). However, climate warming in temperate regions is also associated with a longer vegetation growth period and elevated forest growth rates, which contribute to denser forests and consequent habitat deterioration (Braunisch *et al.* 2014). Moreover, an increase in productivity may raise generalist predator abundance (Elmhagen *et al.* 2010, Pasanen-Mortensen *et al.* 2013), and thus predation risk (Baines *et al.* 2016). Given these potentially opposing effects we urgently require a better understanding of how weather conditions affect grouse reproductive success in order correctly to appraise the potential impact of changing temperature and precipitation patterns on grouse and relate them to the general effects of climate warming on their habitats.

For this purpose, we monitored Capercaillie lekking and reproductive success over a 14-year period to study the seasonal advancement of the lekking season and how weather conditions correlated to reproductive success. Based on the results, we modelled how future weather conditions may affect Capercaillie reproductive success under climate change over the next 20 years.

METHODS

Study area and species

Our study was conducted in the Black Forest, a lower mountain range (max. elevation 1493 m asl) in south-western Germany (Fig. 1). The area is characterized by managed mixed montane forests dominated by Norway Spruce *Picea abies*, Silver Fir *Abies alba*, Beech *Fagus sylvatica* and Scots Pine *Pinus sylvestris*, interspersed with settlements and mountain pastures as well as farmed valleys. The Black Forest supports an isolated population of Capercaillie that has experienced significant declines in abundance and range extent over recent decades and is threatened with extinction (Kämmerle *et al.* 2017, Coppes *et al.* 2019). The Capercaillie is a large-bodied, ground-breeding, precocial bird species, inhabiting semi-open conifer-dominated forests (Klaus *et al.* 1989). The main causes of the population decline in the Black Forest are considered to be human-induced habitat deterioration (Storch 2007), high predation pressure (Kämmerle *et al.* 2017), increasing expansion and intensity of human recreational activities in their habitats (Coppes *et al.* 2017, Kämmerle *et al.* 2017), and climate change (Braunisch *et al.* 2013, 2014).

Timing of reproduction

To detect a potential seasonal shift in the reproductive season, we determined the timing of peak lekking activity, based on the presence of hens at the lekking sites, observed copulations and the daily activity of the males, for each year. These data were derived from observations made during the annual lek counts that have been continuously conducted by hunters, ornithologists and state forest personnel across the whole study area for the purpose of population monitoring (Coppes *et al.* 2019). To determine the yearly peak in lekking activity, lekking sites were monitored every third day over several weeks, during favourable weather conditions (i.e. no precipitation and little wind). In Capercaillie, mating activity is restricted to a few days where the hens are present at the lek, so this peak of lekking activity is a good indicator for the onset of the reproductive period. We applied the methods of Wegge and Rolstad (2017) and defined the yearly peak in lekking activity based on sightings of mating and hens at four lekking sites in our

study area. If the peak in lekking activity encompassed several days, we used the median in our analysis.

Surveys of reproductive success

To survey Capercaillie reproductive success, a total of 30 line transects (mean length: 5.7 km, total: 171 km) were assigned to areas of Capercaillie occurrence in the study area (Fig. 1) and surveyed annually between 2006 and 2019 (14 years). Surveys were conducted in the northern part of the species' range (Coppes *et al.* 2019) with line transects located in open-forest habitats (as of 2006) along linear ecotone structures (i.e. canopy gaps, moor edges, stand edges), which are typical Capercaillie habitats in the region (Schroth 1991, 1994). As males and hens without broods use different habitats than hens with broods (Rolstad *et al.* 1988, Storch 1993), the line transects were placed in a range of suitable Capercaillie summer habitats. Line transects were mapped and annually relocated using handheld GPS devices together with aerial imagery. Transects were surveyed once per year by one experienced observer who walked quietly along the transect and recorded all sightings of Capercaillie. For each sighting, sex and age class (adult vs. chick) were determined. Surveys took place in August and the first half of September, while trying to map individual transects at the same time every year, depending on weather conditions, as surveys were restricted to days without precipitation. During surveys, double sightings of the same individual birds were noted and excluded from the analysis.

From the observations of adult birds and chicks, four metrics of reproductive success were calculated: (1) the brood size (i.e. mean number of chicks per observed brood; calculated for all years with three or more broods); (2) the mean number of chicks per hen (i.e. the numbers of observed chicks divided by the number of adult females; females from here on referred to as hens); (3) the proportion of all hens that were observed with chicks; (4) the sex ratio of male to female chicks (as number of male chicks/number of female chicks). For the analysis we only considered years in which at least 10 hens were observed, as this ensures a robust index of breeding success (Naturvårdsverket, M. Hörnell-Willebrand pers. comm.).

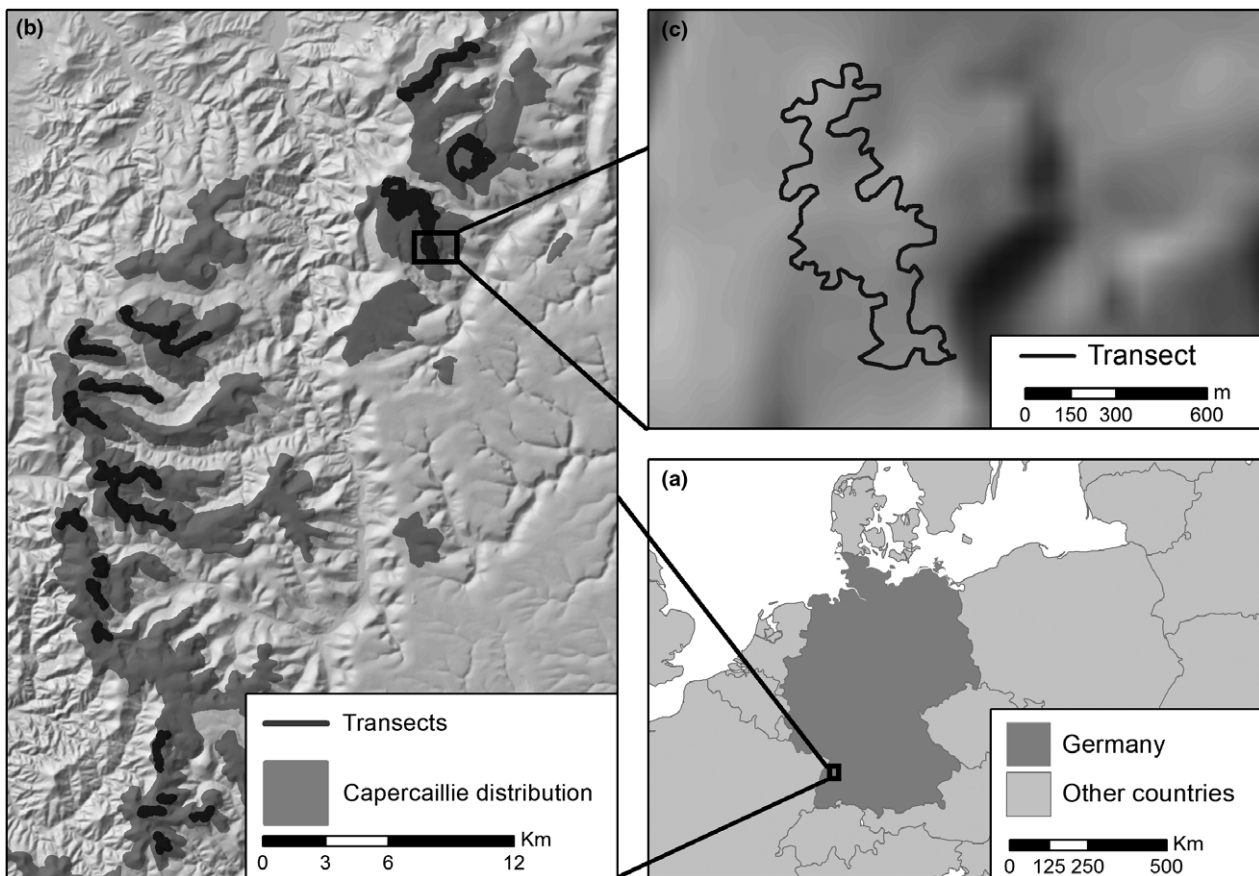


Figure 1. Location of the study area in the Black Forest mountain range in Germany (a) and of the transects within the study area (b). (c) Example of a transect used in this study. Transects were located along linear ecotone structures and surveyed once a year by an experienced observer.

Environmental covariates

Daily values of weather conditions (average temperature (°C) and sum of precipitation (mm)) during the breeding season for each year were obtained from the governmental weather station closest to the survey transects (DWD station Freudenstadt; coordinates WGS: 48°27'13.68"N, 8°24'32.4"E; mean distance to transects: 16 km (sd = 5.8)). We defined a set of distinct time periods over which we aggregated weather predictors because Capercaillie reproductive success is hypothesized to be influenced by weather conditions before copulation (i.e. by affecting vegetation and thereby the body condition of the hens (Moss *et al.* 2001)), during incubation (i.e. extreme weather events or longer cold spells affecting hen behaviour (Klaus *et al.* 1989, Moss *et al.* 2001)) as

well as in the first weeks after hatching (i.e. by influencing insect food sources and thermal regulation of chicks (Klaus *et al.* 1989, Moss 1997, Picozzi *et al.* 1999)). We considered 2-week windows starting 4 weeks prior to the peak of lekking activity and extending 12 weeks after the peak in lekking activity (Fig. 2). We also aggregated the 2-week windows to larger time periods, considering the 4 weeks prior to the peak in lekking activity (i.e. to represent conditions prior to copulation), the 8 weeks after the peak (i.e. to represent conditions during incubation and the first weeks after hatching), 6–12 weeks after the peak (i.e. to represent the first weeks of life of chicks after hatching), and across the whole reproductive season (i.e. 4 weeks prior to 12 weeks after the peak). For each time period we calculated the mean daily temperature, the sum of precipitation volume

(mm) and the number of days with precipitation (i.e. all days with > 0 mm precipitation).

Statistical analysis

In a first step we visualized temporal trends in reproductive success (Fig. 3) and in the time of peak lekking activity over the study period (Fig. 4), fitted a trend line using a linear regression and extracted the coefficient and standard error of the slope (as advancement in days/year). We compared advancement in peak lekking activity with a fitted trend for advancements in vegetation development based on a phenological time series of the date of full apple *Malus domestica* blossom (> 50% of blossoms open) collected for the same region by the state institute for horticulture from 1962 to 2017 (F. Ruef LVWO-WE 2020, unpublished data; Fig. 4). The date of full apple blossom is considered a standard indicator for the onset of spring and thus of overall phenological advancement.

Given our short study period ($n = 14$ years), we chose an exploratory approach to test whether reproductive success was correlated with weather conditions and to identify the combination of environmental predictors that best explained its variation. Specifically, we set up a list of candidate models potentially explaining our reproductive metrics:

- univariate models for each seasonal time period and each predictor ($3 \times 12 = 36$ options);
- models containing all pairwise combinations of temperature and precipitation during the different time periods – owing to their strong pairwise correlations, the number of days with precipitation and the precipitation volume in a given time period were considered separately (i.e. each separately paired with a temperature predictor, resulting in 392 possible combinations);
- models containing all possible two-way interactions between temperature and precipitation predictors, but only considering pairs in the same time window (28 combinations), because we expected chicks to be particularly vulnerable during wet and cold conditions (Klaus *et al.* 1989).

We fitted linear regression models for brood size (value range: 1–2.25), the mean number of

chicks per hen (0.36–1.11) and the sex ratio of chicks (0.17–1.38), and beta regression models for the proportion of hens with chicks (0.15–0.68). We fitted models for each response and predictor combination (456 options per reproductive metric). We excluded the year 2017 from the analysis because fewer than 10 hens were observed. For mean brood size, we did not calculate mean values for the years 2016 and 2017 because fewer than three broods were observed in those years. Due to the limited sample size, we employed a two-step model selection procedure to identify the most parsimonious model in the set. We first ranked all candidate models by second-order AIC corrected for small sample size value (AICc) (i.e. selected the 'best model' if it had an AICc > 2 units lower than the next best-fitting model; otherwise, we identified a 'best candidate set' including all models within 2 AICc units of the best-fitting model). In the latter case, we ranked the models in the set by their adjusted coefficient of determination as a second metric of model parsimony (i.e. R^2 penalized for increasing number of predictors) and defined the best model as the one with the highest adjusted R^2 value. All analyses were performed using the software R (R Core Team 2019).

Implications of climate change

To assess how future spring weather conditions might affect Capercaillie reproductive success under climate change, we used predicted future weather conditions for the time period from 2020 to 2039 under the Representative Concentration Pathway (RCP) emission scenario RCP 8.5 (Pachauri *et al.* 2014), obtained from the environmental database of the German National Forest Inventory (Dietrich *et al.* 2019). The model underlying these data uses historical daily weather observations of the National German Weather Service (DWD) together with downscaling and regionalization of existing climate and digital terrain models to create temporal and spatial high-resolution weather predictions for Germany (Dietrich *et al.* 2019). We used daily predictions of temperature and precipitation at the Freudenstadt weather station, at which our contemporary data were recorded, and aggregated the daily predictions according to the predictors retained in our final models, under the assumption of a continued advancement in peak lekking activity (i.e. by –

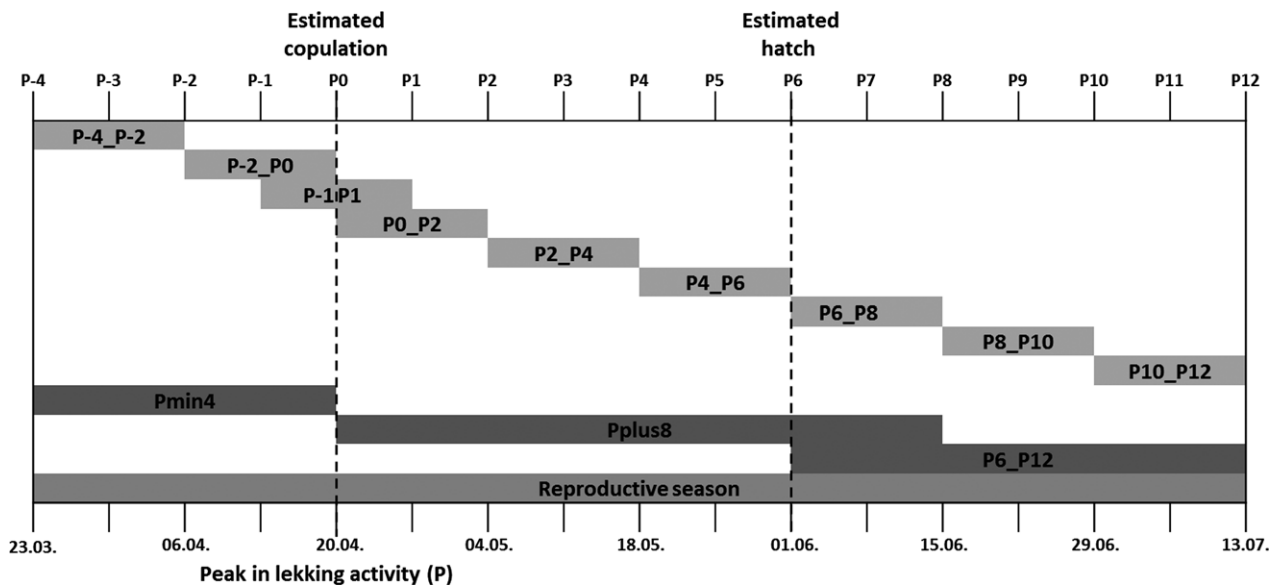


Figure 2. Time periods considered in the analysis of Capercaillie reproductive success. We considered 2-week windows starting 4 weeks prior (P-4) to the peak in lekking activity (P0) and extending 12 weeks after the peak in lekking activity (P12). The bottom row illustrates the time period for an exemplary year with a peak in lekking activity on 20 April.

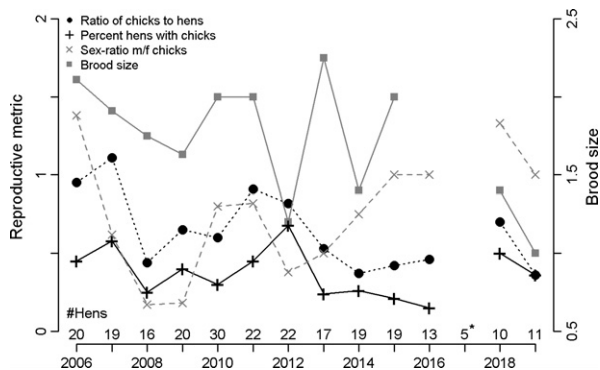


Figure 3. Indices of reproductive success over the study period. The average number of chicks per observed hen ('Ratio of chicks to hens') and the percentage of hens observed with chicks (> 1 denotes more male chicks) in the study area over the study period. The bottom row displays the number of hens observed in each year. Values for the year 2017 were not included in the analysis due to the sample size of < 10 observed hens (*). No mean brood size was calculated for 2016 and 2017 because fewer than three broods were observed in those years.

0.65 days/year, Fig. 4). Finally, we fitted trend lines for the period 2020–2039 to discuss possible implications for Capercaillie reproductive success given the potential future development in weather conditions.

RESULTS

Temporal shift in peak lekking activity

We observed an advance in peak lekking activity from late to mid-April (Fig. 4). The fitted trend line corresponds to a shift of 9 days over a period of 14 years, or -0.65 days/year ($se = 0.30$; $P \leq 0.05$). This was accompanied by a trend towards slightly lower mean temperatures during and after the peak in lekking activity and slightly higher mean temperatures in the first 6 weeks after hatching, but neither of these trends was significant ($P \geq 0.05$). Similar trends were detected for the volume of precipitation, albeit with large variance (Fig. 4), with more precipitation during and after the peak in lekking activity and drier conditions in the first 6 weeks after hatching ($P \geq 0.05$).

Weather conditions correlating with reproductive success

Mean brood size during our study was 1.72 chicks ($sd = 0.40$). The indices for reproductive success had means of 0.64 ($sd = 0.24$) for the mean number of chicks per hen and 0.37 ($sd = 0.16$) for the proportion of hens with chicks. The mean sex

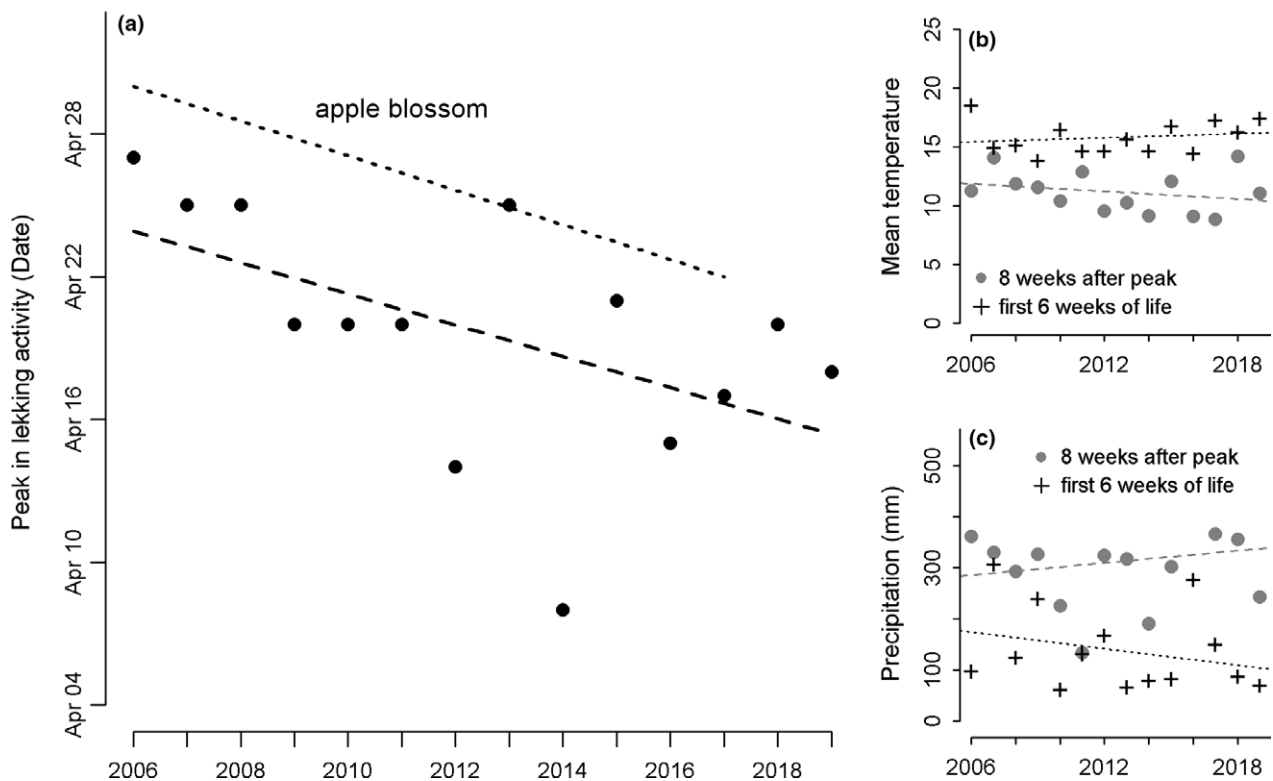


Figure 4. Observed trend in the time of peak lekking activity over the study period (a; trend line corresponds to a shift of -9 days (i.e. an advance) over 14 years, or -0.65 days/year) in comparison with a fitted trend for the seasonal advancement in vegetation development, measured as the date of full apple blossom in the state (F. Ruef LVWO-WE 2020, unpublished data). Small plots show associated weather conditions such as temperature (b) and precipitation volume (mm) (c) during the breeding season for both the first 8 weeks after peak lekking activity (incubation and first weeks after hatching) and the first 6 weeks of chick life (approximately the first 6 weeks after hatching).

ratio favoured female chicks at 0.76 (sd = 0.39). We found unequivocal support (i.e. $\Delta\text{AICc} > 2$) for 'best models' explaining two of four reproductive metrics (chicks per hen; % hens with chicks; Table 1) but there were several candidate models within $\Delta\text{AICc} \leq 2$ for brood size (7) and sex ratio (11), which we additionally ranked by their adjusted R^2 values (Tables S1 and S2). See Table 1 for an overview of final models. All predictors in the final models had significant ($P < 0.05$) effects. The mean temperature across the breeding season was retained in all best models and was positively associated with all measures of reproductive success (Fig. 5). Higher mean temperatures during the season were correlated with higher reproductive success (i.e. larger brood size, more hens with chicks and more chicks per hen, Table 1). All models also contained a predictor of precipitation, with precipitation volume during the

first weeks after hatching being associated with a smaller brood size (Fig. 5), whereas the precipitation patterns prior to mating were correlated with the overall abundance of chicks (Fig. 5d,f). Temperature and precipitation had similar effect sizes across all final models (Figs 5 and 6). In the candidate set for brood size, the temperature during incubation (2 weeks following peak in lekking) and the temperature during the weeks preceding the peak in lekking activity were retained (Table S1) in the best-fitting model, both with positive effects on brood size. In addition, several precipitation predictors were retained with positive or negative slope and no consistent pattern with regard to brood size. The next most competitive model ($\Delta\text{AICc} = 0.071$, $\Delta R^2 = 0.003$; Table S1) showed a positive effect of temperature during incubation and a positive effect of precipitation in the 4 weeks prior to mating.

Table 1. Model summaries of the best models explaining different reproductive metrics (A: mean brood size, B: the mean number of chicks per hen, C: the percentage of hens with chicks, D: the male/female sex ratio of broods) as a function of weather covariates, aggregated over different time periods (Fig. 2).

Predictor	Estimate	se	P-value	ΔAICc	Adj. R^2
<i>Model A: brood size</i>					
Intercept	−2.103	1.258	0.129	0.071	0.53
Mean Temp Season	0.340	0.104	0.010		
Prec. Vol. P6_P8	−0.012	0.004	0.014		
<i>Model B: chicks/hens</i>					
Intercept	−1.751	0.543	0.009	2.810	0.68
Mean Temp Season	0.208	0.044	0.001		
Prec. Vol. P-4_P-2	−0.005	0.002	0.015		
<i>Model C: % hens with chicks</i>					
Intercept	−5.142	1.465	0.001	3.092	0.64
Mean Temp Season	0.475	0.122	<0.001		
Prec. Days P-4_P-2	−0.161	0.036	<0.001		
<i>Model D: sex ratio, m/f</i>					
Intercept	−19.433	6.224	0.012	−0.199	0.67
Mean Temp. P6_P12	1.806	0.510	0.006		
Prec. Vol. P6_P8	0.337	0.103	0.010		
Mean Temp.*Prec. Days	−0.030	0.009	0.006		

The best model was defined as the model that had the highest adjusted R^2 value within a $\Delta\text{AICc} \leq 2$ candidate set. The predictor column indicates the predictors: Mean Temp. is average temperature, Prec. Vol. indicates the total volume of precipitation, and Prec. Days indicates the number of days with precipitation in the time period. The time periods are as indicated in Fig. 2: season refers to the entire reproductive season, P-4_P-2 refers to the 2 weeks between 4 and 2 weeks before the peak in lekking activity, and P6_P8 refers to the 2 weeks 6–8 weeks after the peak in lekking season. The coefficient estimates, associated standard errors and P-values are provided, as well as the ΔAICc to the second highest-ranked model, except for model D, where ΔAICc indicates the difference to the top ranked model (i.e. the final model presented was ranked third based on ΔAICc but highest based on Adj. R^2).

Weather conditions correlating with chick sex ratio

The best model explaining the sex ratio of chicks contained an interaction between mean temperature and the number of days with precipitation across the reproductive season. Drier and warmer years were associated with more male than female chicks, whereas in wetter and colder years the sex ratio was in favour of female chicks (Fig. 6). In the candidate set for sex ratio, temperature and precipitation during the weeks after hatching were identified as important in most models of the set (e.g. 6–12 or 6–8 weeks after the peak in lekking activity; Table S2), with higher temperatures being associated in most models with more male chicks, and increasing precipitation with more females (Table S2), thus supporting the pattern predicted by the final model for sex ratio. The next most competitive model in the set ($\Delta\text{AICc} = -0.199$, $\Delta R^2 = 0.120$) included temperature and the number of days with precipitation during the first 6 weeks after hatching.

Future development in spring weather conditions

Assuming the seasonal advancement in peak lekking activity to continue by -0.65 days/year (i.e. the trend line estimate) and adjusting the relevant time frames for weather variables accordingly, we found no significant change in key weather conditions during the reproductive season over the period 2020–2039. Mean temperature and the number of days with precipitation during the whole reproductive season were predicted to be stable, albeit with high interannual variation (Fig. S1). However, there was a slight trend towards higher precipitation volume during the first weeks of chick life (6–8 weeks after copulation (P6_P8)) and less precipitation prior to copulation (4 weeks before copulation (P-4_P-2)) (Fig. S1).

DISCUSSION

We investigated the timing of reproduction and reproductive success in relation to weather

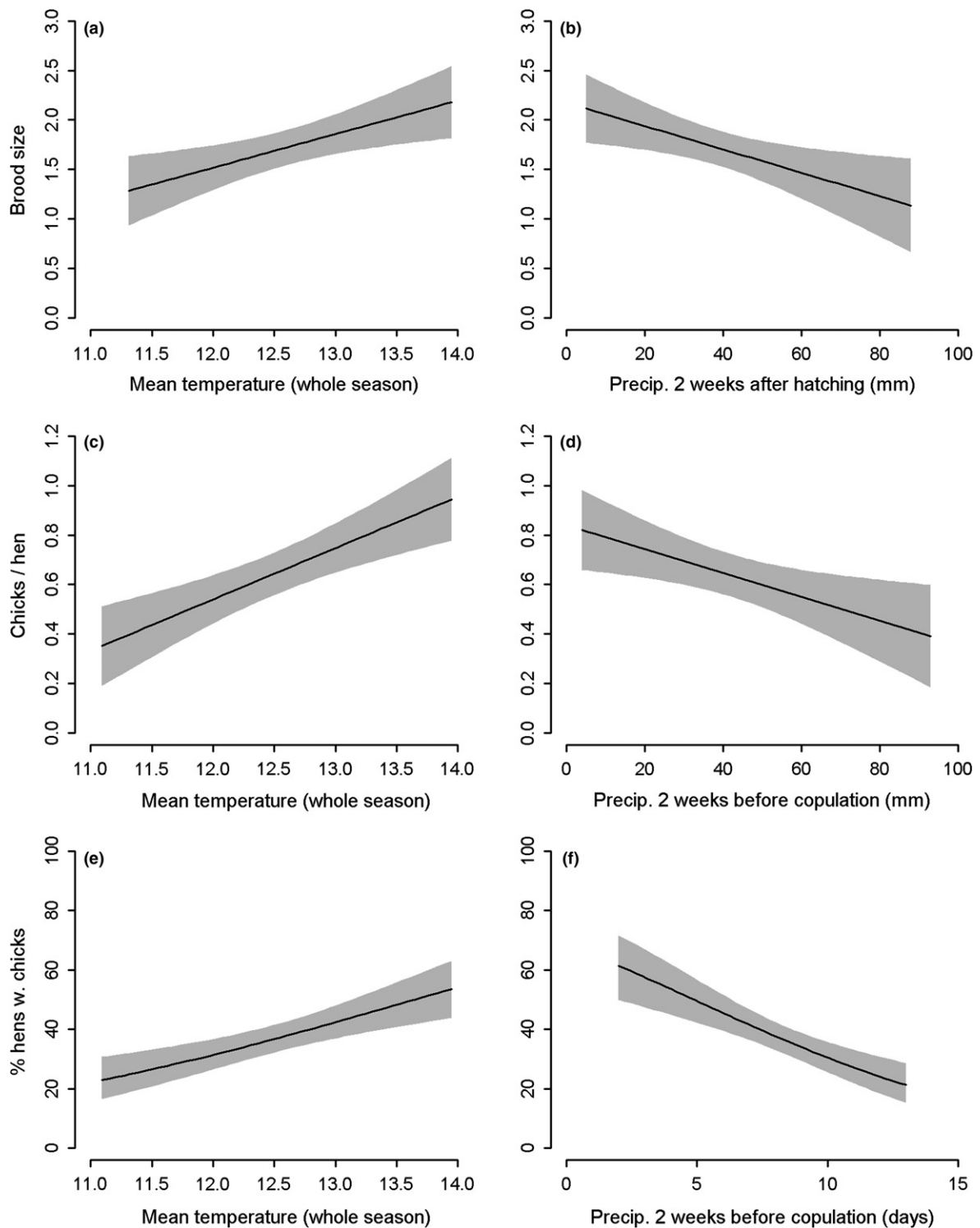


Figure 5. Effect plots of the best models explaining variation in Capercaillie brood size (a, b), the mean number of chicks per hen (c, d) and the proportion of hens with chicks (e, f) in relation to the mean temperature of the whole reproductive season and precipitation in different time windows during the reproductive season. Time windows displayed are 4–2 weeks prior to the peak in lekking activity (i.e. P-4_P-2) and approximately the first weeks after hatching of chicks (P6_P8; 6–8 weeks after the peak in lekking activity). Mean slope estimates are presented with 95% confidence intervals. For time periods see Methods and Figure 2.

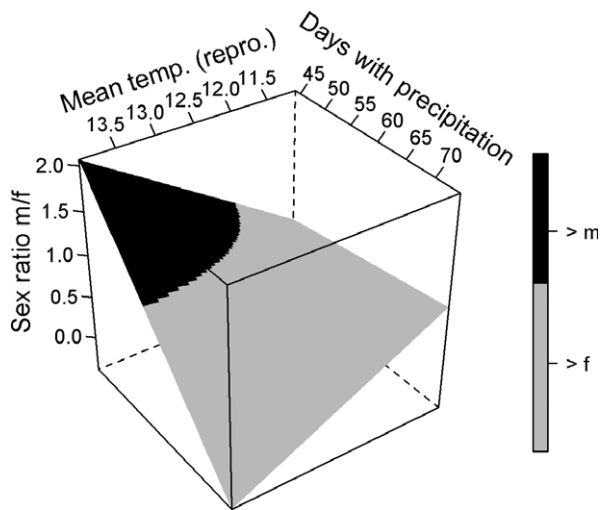


Figure 6. Effect plot of the interaction between the number of days with precipitation and the mean temperature over the whole reproductive season explaining the variation in the sex ratio between male and female Capercaillie chicks in the study area as predicted by the best model. Values < 1 denote a sex ratio in favour of female chicks (grey) in wetter and colder years.

conditions under climate change because rapidly advancing spring warming bears the risk of mistimed reproduction (Visser *et al.* 2004, Carey 2009). Although some species appear capable of a rapid phenological advancement due to climate change (e.g. Crick & Sparks 1999, Liebezeit *et al.* 2014), this may not always be the case (e.g. Both *et al.* 2006) and flexibility is unlikely to be limitless. We report a continuous advance in peak lekking activity of Capercaillie over a period of 14 years, corresponding to an advancement of -0.65 days/year, which is well within the range of phenological advancement in other bird species (Crick & Sparks 1999, Liebezeit *et al.* 2014) and closely matches the phenological advancement of vegetation in the region (indicator: date of full apple blossom $\Delta \approx -0.66$ days/year; Fig. 3). The seasonal advancement we found is fast compared with what was found in other Capercaillie populations, including those in Scotland (1981–1999: -0.23 days/year (Moss *et al.* 2001)), southern Norway (1979–2017: -0.12 days/year (Wegge & Rolstad 2017)), the French Pyrenees (1979–2010: -0.37 days/year (Ménoni *et al.* 2020)) and the Voges mountains (1973–2012: -0.38 days/year (Ménoni *et al.* 2012)). Wegge and Rolstad (2017) inferred that Capercaillie cannot match the speed of spring advancement and phenology in southern

Norway, whereas our results suggest that Capercaillie in the Black Forest match the phenological advancement. This difference may be explained by differences in phenological changes at different altitudes or latitudes (Cohen *et al.* 2018) or because our study encompasses only recent years, during which climate change has considerably accelerated (WMO 2019). The advancement we found is, however, similar to that found by Ménoni *et al.* (2020) in the Jura mountains (1977–2006: 0.70 days/year), whose study covers a longer time period as well as a different time period compared with our data. Our analysis of future spring weather conditions (2020–2039) showed no significant expected change in weather conditions during the breeding season over the 20-year period, assuming that the current shift in onset of reproduction continues at the same pace. Our results thus indicate that Capercaillie might be able to maintain constant weather conditions during the relevant season by adjusting the timing of reproduction, were phenological advancement to continue at the current rate. The large interannual variation in predicted weather conditions, and particularly in precipitation, could, however, imply a higher frequency of extreme years with severe – or even complete – losses of broods if cold conditions and heavy precipitation coincide. It is important to note that our projection assumes a continuous yearly advancement of the breeding season and of the corresponding relevant time frames. In reality, however, the timing of reproduction is likely to track annual variation in weather conditions, thus limiting the accuracy of our predictions.

The advance we found in the Black Forest resulted in largely consistent weather patterns during reproduction, but increasingly early in the year. This may indicate that the species is adjusting its reproductive activity to the rapidly changing conditions. At the same time, however, there is a divergent trend in weather patterns towards colder, wetter lekking- and incubation-seasons and drier warmer weeks following chick hatching (Fig. 4), suggesting that the consequences of phenological advancement are clearly more complex than simply reproducing earlier in the year. The timing of lekking (i.e. onset of the breeding season) might also be linked to vegetation phenology, which is supported by the fact that Capercaillie at higher elevations generally start lekking later in the year (Klaus *et al.* 1989, Zeiler 2001).

For grouse in particular, spring weather conditions are often considered critical for successful reproduction (Moss 1985, Klaus *et al.* 1989, Moss *et al.* 2001, Wegge & Rolstad 2017). Baines *et al.* (2016) found that the hatching period of Capercaillie coincided with the peak of biomass of moth caterpillars, an important food source for the chicks. The timing of this peak is likely to change under different spring weather conditions and Capercaillie must adjust by timing their reproduction appropriately. We found indications that the timing of the peak lekking season, and with it the hatching period, is changing, so that weather conditions during the breeding season remain relatively constant across the years. However, the degree of flexibility in timing and its environmental cues remain largely unknown.

The reproductive success we found is relatively low compared with other studies (Moss *et al.* 2001, Baines *et al.* 2004, Wegge & Rolstad 2017), which might be due to differences in the timing of the surveys (i.e. later in the season compared with the other studies) or the methods we used. Monitoring of grouse reproductive success is often performed using trained dogs (Caizergues & Ellison 1997, Moss *et al.* 2001, Wegge & Rolstad 2011, 2017), but in the Black Forest there is no such tradition (Taubmann & Ramlow 2019) and trained dogs were not available for our study, which might have reduced our detection probability. However, reproductive success is generally very low in the Black Forest, which is likely to be the cause of the population decline during our study period (Coppes *et al.* 2019). Despite the highly exploratory nature of our approach, the predictor variable selection in our final models supports the initial assumptions regarding the importance of weather patterns for grouse reproductive success during two time windows. All final models contained precipitation predictors in addition to a temperature predictor, and the selected time windows match those that were initially hypothesized to be relevant. Brood size was negatively associated with precipitation during the first 2 weeks after hatching. It thus appears likely that chick mortality is higher in years with more precipitation during the first weeks after hatching, leading to smaller brood sizes in autumn. In line with our results, previous studies have suggested that grouse chicks are in addition more vulnerable to predation in wetter conditions (Baines 1991, Wegge & Kastedalen 2007). Moss *et al.* (2001) also found that

precipitation after hatching was inversely associated with brood sizes, but not the proportion of hens with broods. Possibly, rainy weather increases the mortality of individual chicks, but less often causes loss of entire broods (Moss *et al.* 2001). However, the small sample size as well as the change in the sign of the slope estimate of precipitation predictors in our set of competing models for brood size (Table S1) suggests that the determinants of successful reproduction are certainly more complex, highlighting the limitations of a correlative approach as applied here.

In addition, more precipitation prior to lekking was associated with fewer and smaller broods. Swenson *et al.* (1994) found similar results for Hazel Grouse *Bonasa bonasia* but concluded that this should not be the case for the larger grouse species. Moss and Watson (1984) found that reproductive success of Rock Ptarmigan *Lagopus muta* in Scotland was determined by the physical condition of the hen prior to laying. Physical condition is affected by the availability of nutrient-rich food, which in turn is affected by winter conditions. Similarly to our results for Capercaillie, Novoa *et al.* (2008) found Rock Ptarmigan reproductive success in the French Pyrenees to be affected by weather conditions both before egg-laying and after hatching of the eggs. Wet and cold conditions in the pre-laying phase appear negatively to affect feeding conditions and female body condition before copulation, leading overall to fewer (or smaller) successful broods (Klaus *et al.* 1989).

We could only include the peak of the lekking season as a proxy for the time of copulation and do not have data on the hatching dates of the chicks per year (to avoid detrimental effects of disturbance, Capercaillie habitats were not entered during the time after lekking). We therefore have no information on variation in the exact timing of hatching among years, or on replacement broods (i.e. after losing the first brood in an early stage, some hens make a second brood later in the season (Klaus *et al.* 1989)). For replacement broods, our generalizations about the timing of breeding would not agree with the timing of copulation and hatching (Moss *et al.* 2001). Nonetheless, given the small sample and the large among-year variance, our findings are surprisingly clear and support the general assumptions about the importance of spring weather patterns for grouse reproduction.

In accordance with previous work (Moss *et al.* 2001, Wegge & Rolstad 2017) we found

unequivocal support for warm spring conditions as a correlate of all measures of reproductive success. However, warming may also have unforeseen and complex consequences for grouse (Selås *et al.* 2011). For instance, we observed that cold and wet springs favoured female-biased sex ratios (Fig. 6), perhaps because years with high environmental stress (cold and high amounts of precipitation) cause higher mortality in male chicks, for which the weight gain and consequential energy demand is higher due to sexual dimorphism (Klaus *et al.* 1989, Hörnfeldt *et al.* 2008). Unfavourable environmental conditions may affect the sexes differently and result in different patterns in the sex ratio of adult birds. Declining populations are reportedly characterized by a female-biased sex ratio (Wegge 1980, Saniga 2001). Similarly, Augustine *et al.* (2020) found a population decline only for Capercaillie males and not for hens in east-central Switzerland. A trend towards overall higher mean temperatures and increasingly warm springs may thus also assist declining grouse populations. It is important to note, though, that due to the small sample size, our survey methods, as well as the low reproductive success (i.e. few chicks found) in our study, small changes in chick counts can greatly affect the results.

The exact consequences of changing weather patterns for grouse populations are difficult to predict because they affect reproduction not only directly, but also indirectly by altering habitat suitability, adult as well as chick food availability or predator abundance, with potentially contrasting effects. Integrating these differing effects in mechanistic models may allow elucidation of additive or compensatory effects of climate change-induced weather changes on grouse populations and provide a basis for assessing future possibilities for grouse conservation.

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AUTHOR CONTRIBUTION

Joy Coppes: Conceptualization (equal); Formal analysis (supporting); Methodology (equal); Project administration (equal); Supervision (equal); Writing-original draft (lead); Writing-review & editing (equal). **Jim-Lino Kämmerle:** Data curation (lead); Formal analysis (lead); Visualization (lead); Writing-original draft (equal); Writing-review & editing (equal). **Karl-Eugen Schroth :** Conceptualization (equal); Investigation (lead); Methodology (equal); Resources (equal); Writing-review & editing (equal). **Veronika Braunisch:** Conceptualization (equal); Funding acquisition (equal); Methodology (equal); Supervision (equal); Writing-review & editing (equal). **Rudi Suchant:** Conceptualization (equal); Funding acquisition (lead); Methodology (equal); Project administration (lead); Supervision (equal); Writing-review & editing (equal).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Predictions of weather covariates retained in the best models for the time period 2020–2039, assuming climatic changes the IPCC-Representative Concentration Pathway Scenario RCP 8.5, obtained from the environmental database of the German National Forest Inventory (Dietrich *et al.* 2019). Grey lines depict fitted trend lines; all trends were not significant ($P > 0.05$).

Table S1. List of candidate models (with $\Delta AIC_c \leq 2$ to the best model) for explaining mean capercaillie brood size at the study sites in the northern Black Forest Germany between 2006 and 2019.

Table S2. List of candidate models (with $\Delta AIC_c \leq 2$ to the best model) for explaining the sex-ratio of capercaillie chicks at the study sites in the northern Black Forest Germany between 2006 and 2019.