WILDLIFE BIOLOGY

Research

Long-term trends of reproductive success of black grouse *Lyrurus tetrix* in the southern Swiss Alps in relation to changes in climate and habitat

EDITOR'S CHOICE

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Wildlife Biology
2022: e01022
doi: 10.1002/wlb3.01022

Subject Editor: Christian A Hagen
Editor-in-Chief: Ilse Storch
Accepted 11 January 2022

Breeding success of an Alpine black grouse *Lyrurus tetrix* population in southern Switzerland was monitored from 1981 to 2020. This long-term dataset allows exploring relationships of reproductive rates with climate and habitat, which have shown marked changes during this period. Over the 40 years, the average elevation of black grouse breeding sites increased by around 100 m in central/southern Ticino but showed only a slight increase in northern Ticino, where black grouse occur at higher elevations. Average reproductive rates in northern Ticino remained constant throughout the study period but declined in central/southern Ticino. Relationships between reproductive success and weather as well as habitat variables were analysed with a multiple regression model. Temperature during the early chick-rearing phase and the time of egg-laying was positively correlated with reproductive rate. Correlations between reproductive rates and precipitation were less clear, and only small proportions of the variance in reproductive rates could be explained by precipitation. Brush forest explained the greatest amount of variation in reproductive rate (6.2%). Forest, alpine agricultural areas and unproductive vegetation all showed a positive relationship with reproductive rate, but the proportion of the variance explained was small. Year (5.1%) and its interaction with region (2.3%) explained considerable amounts of the variance. While in northern Ticino reproductive success did not show a negative trend when correcting for weather and habitat changes, there remained a negative trend over the years in central/southern Ticino. Despite the positive correlations of reproductive rate with temperature, increasing temperatures do not appear to have improved reproductive success, likely as a result of habitat changes that forced black grouse towards higher elevations. Changes in reproductive success were limited to the southern region, indicating deteriorating conditions at the edge of the distribution range.

Keywords: climate change, habitat change, reproductive success

Weather conditions are important factors affecting the demography of animal populations and as a result population trends and ultimately the distribution of species.

Weather conditions are determined by the local climate, and with the increasing speed of climate change populations may not be able to track changes in meteorological conditions (Crick 2004, Pearce-Higgins and Green 2014). Mountain ecosystems are particularly vulnerable to the effects of climate change because mountains warm at a higher rate than lowlands (Pepin et al. 2015). Moreover, mountain areas are highly seasonal environments, to which specialist species are well adapted. Small changes in climate could have large effects on the seasonality (e.g. snow melt and associated vegetation growth) and disrupt reproductive phenology of animals (Scridel et al. 2018).

In mountainous environments, the season suitable for reproduction is usually short (Hille and Cooper 2015). In non-migratory birds like grouse (Tetraoninae), chicks need to achieve a body condition suitable to survive winter, when food availability and quality decrease rapidly. Studies on several grouse species have identified critical periods during the reproductive cycle: in the pre-laying period, hens require easily digestible protein-rich food from plants which grow only above a certain temperature (western capercaillie *Tetrao urogallus*, black grouse *Lyrurus tetrix*: Siivonen 1957; red grouse *Lagopus lagopus scoticus*; rock ptarmigan *L. muta*: Moss et al. 1974, Moss and Watson 1984; rock ptarmigan: Novoa et al. 2006). Later in the season, chicks require a sufficient supply of invertebrates, and timing of hatching dates in relation to peak insect abundance is important (Wegge et al. 2010, Wegge and Rolstad 2017). Grouse chicks are particularly vulnerable to direct weather effects in their first days of life, when their thermoregulatory system is not yet fully developed (Höglund 1955, Rajala 1962, Marti and Bossert 1985, Ludwig 2009, Ludwig et al. 2010).

Changes in climatic parameters can affect the demography of grouse directly or indirectly by changes in their habitats (Scridel et al. 2018). Thus, knowledge of demographic processes and how they change over time is essential to understand possible effects of changes in climate and habitat. However, few long-term studies on grouse exist in Europe. Several studies have documented earlier lekking behaviour in capercaillie over time but how this affected reproductive success remained unclear (Wegge and Rolstad 2017, Coppes et al. 2021). A review of results from 16 countries in Europe, covering a time period of 80 years (1930–2012), showed a decline of reproductive success of western capercaillie and black grouse (Jahren et al. 2016). The authors attributed the decline to a combination of changes in climate and land use as well as an increase in generalist predators. Jahren et al. (2016) was limited to northern and lowland central Europe, with few studies from black grouse populations in the Alps. Climatic conditions and land use, however, differ in many respects from those in lowland and high-latitude regions. Temperature or precipitation may vary at different elevations or show different seasonal patterns, which again may affect demographic parameters such as survival or reproductive output in mountain ecosystems (Moss et al. 2001). Higher temperatures lead to an expansion of forest towards higher elevations, but increasing forest cover is also a result of changes in human land use, in particular the abandonment of farming (Gehrig-Fasel et al. 2007). Unlike bird populations in lowland areas, bird populations in mountain ecosystems may react to changes in climatic conditions by changing their distribution towards higher elevations to retain a favourable climatic niche, which in the Alps has been documented for rock ptarmigan (Pernollet et al. 2015) as well as black grouse (Knaus et al. 2018).

In the southern Swiss Alps black grouse populations have been monitored continuously since 1981. The monitoring programme covers a period of increasing temperature (Rebetez and Reinhard 2008), associated with an advancement of the growing season in spring (Chmielewski and Rötzer 2001). An earlier analysis of data from the monitoring programme, covering the period 1981–2002, identified temperature during the hatching period of chicks as critical for determining reproductive success (Zbinden and Salvioni 2004). This finding was true for more southern and more northern parts of the study area, which differed in elevation. The now 40 years of the study provide a framework to explore changes in reproductive success in relation to changes in climate and habitat. Specifically, we first describe long-term trends in elevational distribution of black grouse breeding sites as well as trends in temperature at these sites, second, we analyse relationships of reproductive success with weather and habitat. We compare trends in two different parts of the study area differing in elevation and discuss the results in relation to changes in climate and habitat.

Methods

Study area

The black grouse monitoring project run by the 'Ufficio della Caccia e della Pesca del Cantone Ticino', the Cantonal Wildlife Office, covers the distribution of black grouse in the Canton of Ticino in southern Switzerland (central coordinates 46.2°N, 8.8°E). The Canton of Ticino covers an area of 2812 km^2 and stretches from the main ridge of the Alps south to the foothills at the border to Italy, where the black grouse reaches the edge of its range. The study area was divided into two regions, 'northern Ticino' and 'central/southern Ticino'. The border between these two regions corresponds to the limit between the biogeographic regions 'southern Alps' and 'southern Ticino' determined based on faunistic and floristic criteria (Gonseth et al. 2001).

Bird data

Bird data were collected annually from 1981 to 2020. Reproductive rate, measured as number of juveniles per total number of hens, was determined in the second half of August/early September, when chicks have survived the high mortality during the first two weeks of life (Hannon and Martin 2006). Data were collected by hunters owning well-trained pointing dogs (mostly English setter or Pointer).

Areas with known occurrence of black grouse were searched and all observations of hens with and without chicks noted. In mid-August almost all chicks are able to fly, which allows reliable counts of the number of chicks per hen. Observers noted the geographical coordinates and elevation of each observation of a hen. As the precise elevation and coordinates were often lacking, in particular during the first decades of the study, the median elevation of the kilometre square of the Swiss geographical grid was used. In total, the data set consisted of 9090 observations of hens. The effort of hunters to carry out surveys increased over time, resulting in a higher number of kilometre squares with records. However, surveys were well distributed across the study area in each of the four decades, minimising any geographical bias (Fig. 1). Sample size was larger in northern Ticino, with data from an average of 71 squares (range 14–136) per year, compared to 47 squares (26–80 squares) in central/southern Ticino. The study squares covered altitude ranges of 1150–2710 m a.s.l. for northern and 990–2230 m for central/southern Ticino.

Weather data

Weather data were provided by the Federal Office for Meteorology and Climatology MeteoSwiss for the weather station of Locarno-Monti, which lies at 367 m in central Ticino (46°70'21''N, 08°47'15''°E). The following parameters were used based on measurements at one-hour intervals: mean temperature, total precipitation during daytime (06:00–18:00 h) and during the night (18:00–06:00 h). Temperature values of Locarno-Monti were adjusted to the mean elevation of kilometre squares with hens for each year and separately for the two regions. Calculations were based on the assumption of a decrease of 0.7°C per 100 m increase in elevation (Ozenda 2002, Veit 2017). A comparison with the values from different weather stations in the study area (which, however, did not cover the whole study period) had shown that this calculation can be considered valid for the summer period (Zbinden and Salvioni 2004).

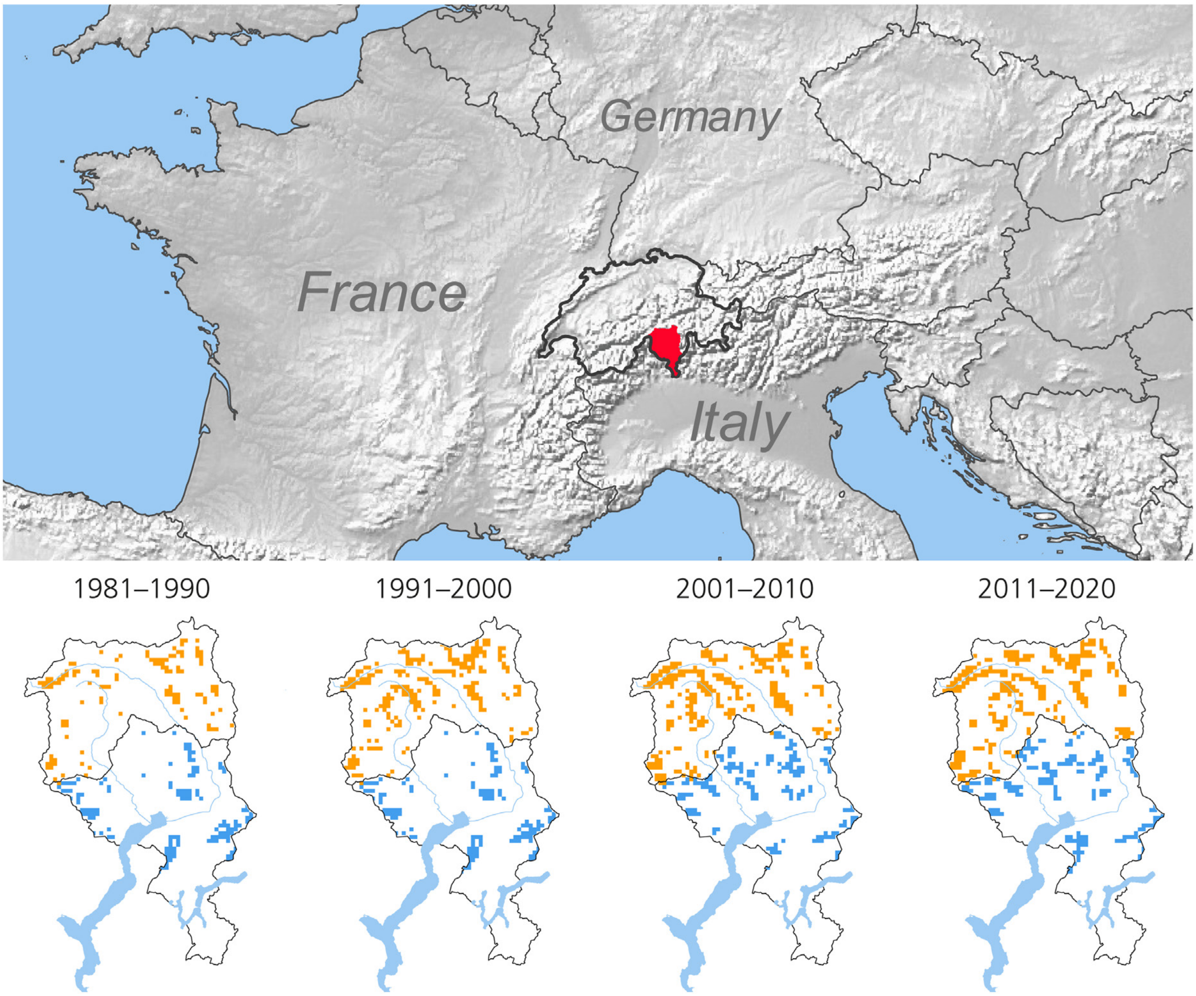

Figure 1. Top: location of the Canton of Ticino (red) in Switzerland in the context of Europe. Bottom: distribution of surveyed kilometre squares in the four decades of the study period. Orange: northern Ticino, blue: central/southern Ticino.

Habitat data

Habitat information was retrieved from the Swiss land-use statistics, published by the Federal Statistical Office (Bundesamt für Statistik 2017). The following land-cover variables considered relevant for black grouse habitats were selected from the categories defined by the NOAS04 nomenclature (Bundesamt für Statistik 2013): forest (closed and open forest), brush forest, alpine agricultural areas (alpine pastures and meadows), unproductive vegetation (scrub, unproductive grass and shrubs etc.). For all variables, the percentage area in each surveyed kilometre square was calculated. Land-cover data were available for four time periods, collected over the years 1979–1985, 1992–1997, 2004–2009, 2013–2018, and were allocated to the bird data according to the last year of the land-use statistics: 85 for data 1981–1990, etc.

The composition of the four habitat categories varied between northern and central/southern Ticino with lower percentages of forest and brush forest and higher percentages of alpine agricultural areas and unproductive vegetation in the north (Fig. 2). In northern Ticino, forest cover in the surveyed squares increased by almost 10% over 40 years, whereas the other categories showed slight declines. In central/southern Ticino alpine agricultural areas declined in a similar way as in northern Ticino, whereas the already high forest cover hardly changed.

Statistical analyses

All analyses were conducted at the level of region, i.e. using regional mean values of reproductive success and environmental variables for the set of kilometre squares surveyed in a particular year. All analyses were conducted with the software R ver. 4.0.5 (<www.r-project.org>).

To visualise trends in reproductive rate, elevation of hens and temperature, we smoothed the data using a generalized additive model with cubic regression splines. We chose the degree of smoothness by leave-one-out cross-validation (function *gam* from the R-package mgcv, Wood 2006). For visualising temporal trends in habitat variables we used normal linear regressions.

To assess relationships between reproductive success and weather as well as habitat variables we used multiple regression analysis. Reproductive rate is measured as the number of juveniles divided by the total number of hens. An appropriate statistical model for such count data would be a negative-binomial model with the number of juveniles as outcome, the logarithm as link function and the logarithm of the number of hens as an offset. Because in our data the expected value for the number of juveniles was high (> 40, the minimum count), we can expect that the negative distribution is well approximated by a normal distribution. We fitted both the negative binomial model to the number of juveniles and the normal model to the reproductive rate (number of juveniles divided by the number of hens). Indeed, there were no markable differences between the two results as well as between the model fits. We assessed the latter by posterior predictive model checking and by standard residual plots. As effect sizes are easier to interpret from a normal model because they are additive rather than multiplicative, we here present the results from the normal linear model. Numeric predictor variables were year, five-day average temperature for two time points (T1 and T2, below), five-day sum of precipitation for T1 and T2 during daytime and during the night, and percent coverage of the following habitat types: alpine agricultural areas, brush forest, forest and unproductive vegetation.

The time points T1 and T2 were determined by searching for those dates when reproductive rate was most sensitive to changes in temperature. To do so, we obtained regression coefficients of reproductive rate with all possible five-day mean temperature values across the breeding season. We then added a smoother using the method explained above to these regression coefficients and extracted the dates of the two highest peaks as T1 and T2 (Zbinden and Salvioni 2004).

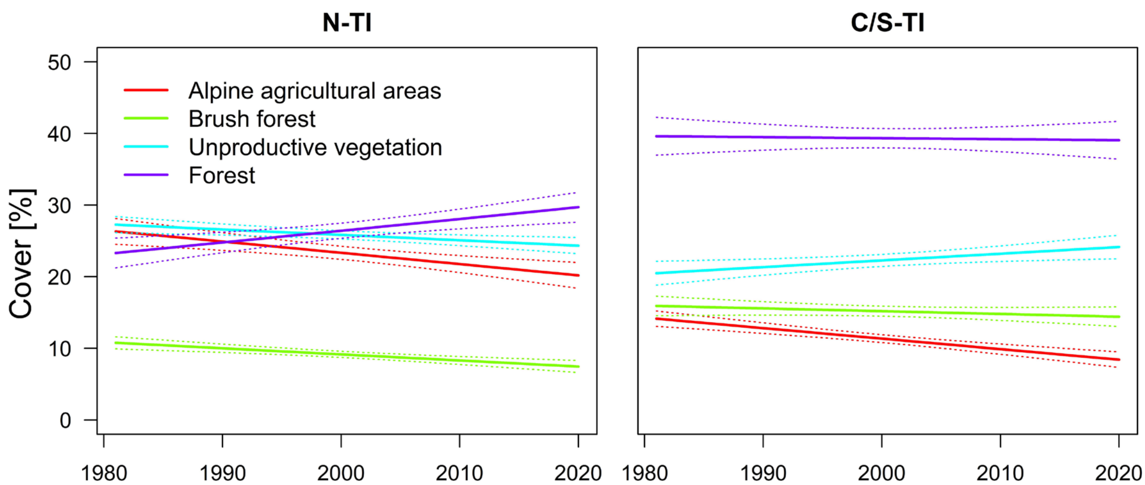

Figure 2. Percentage of surveyed kilometre squares covered by four habitat categories in northern (N-TI) and central/southern Ticino (C/S-TI) 1981–2020. Lines are ordinary linear regression lines with 95% CI.

We started with a model that only included linear effects and no interactions. When plotting the residuals of this model against all predictor variables, a curvilinear relationship was obvious for brush forest cover. Because a curvilinear relationship between reproductive rate and brush forest cover can be explained biologically, we added the quadratic term of brush forest to the model. In this final model, we could not detect obvious linear or non-linear relationships between the residuals and any predictor variable which could indicate missing interactions or non-linear relationships. Therefore, we did not include interactions or other polynomials in the model.

Results

Elevation and temperature at breeding sites

Black grouse hens were recorded at an average elevation of around 1900 m a.s.l. in northern Ticino and between 1600 and 1700 m in central/southern Ticino. In central/southern Ticino the annual average elevation increased by around 100 m from 1981 to 2020 but showed only a slight increase in northern Ticino (Fig. 3).

Average monthly temperatures in the study area increased by 2–3°C over the study period 1981–2020 (Fig. 4a–d, dashed line). The temperature increase at the actual breeding locations of black grouse was lower in both parts of the study area, as indicated by the difference in the slopes compared to the dashed line. In other words, by moving upwards black grouse hens experienced higher temperatures, but this increase was not as large as if they had continued to breed at the same elevation.

Reproductive rates

The long-term average reproductive rate was 2.0 (SD = 0.5) chicks/hen in northern Ticino and did not show a decline (Fig. 4e). However, reproductive rates declined in central/southern Ticino in the early years of the study period and stabilised at the level of northern Ticino from around 2000 (Fig. 4e). Reproductive rates showed marked variation from year to year with a pattern similar to the variations in July temperature (Fig. 4d).

Critical periods in the reproductive cycle

Regression coefficients of reproductive success on five-day average temperatures show two marked peaks with highest values in early July for central/southern Ticino and mid-late July for northern Ticino, corresponding to the early chick-rearing phase (Fig. 5). A smaller peak is visible around 1 June, coinciding with the time of egg production/egg laying (Discussion). Temperature at the peak dates in June and in July (T1 and T2, small arrows in Fig. 5) were used in the model, separately for the two regions.

Reproductive rate in relation to weather and habitat

Reproductive rate was associated with both weather and habitat variables (Table 1, Fig. 6, 7). Temperature at both time points (T1 and T2) was positively correlated with reproductive rate. Correlations between reproductive rates and precipitation were less clear, and only small proportions of the variance (< 1%) in reproductive rates could be explained by precipitation.

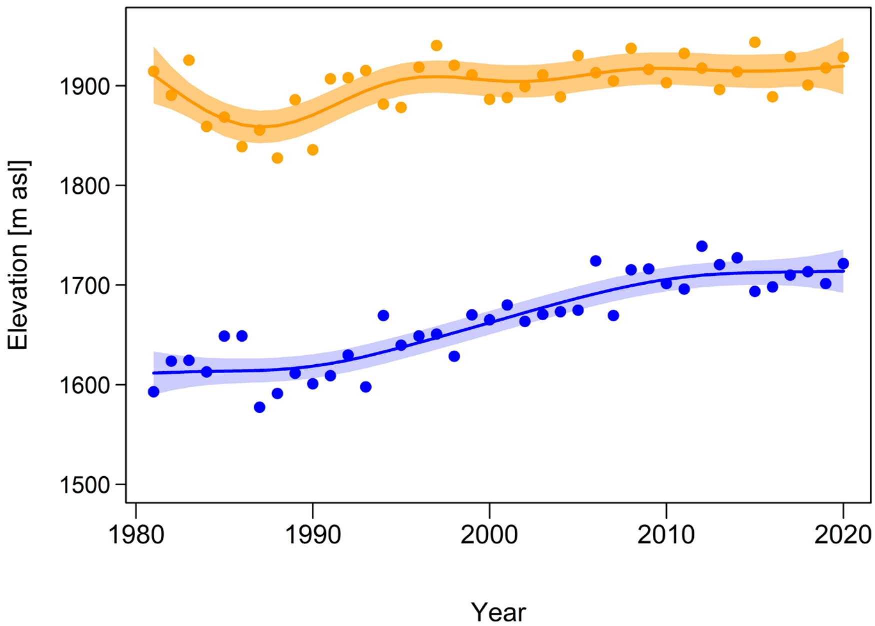

Figure 3. Average elevation of kilometre squares with observations of black grouse hens in northern Ticino (orange) and in central/southern Ticino (blue). Smoothed regression lines with 95% uncertainty intervals are given.

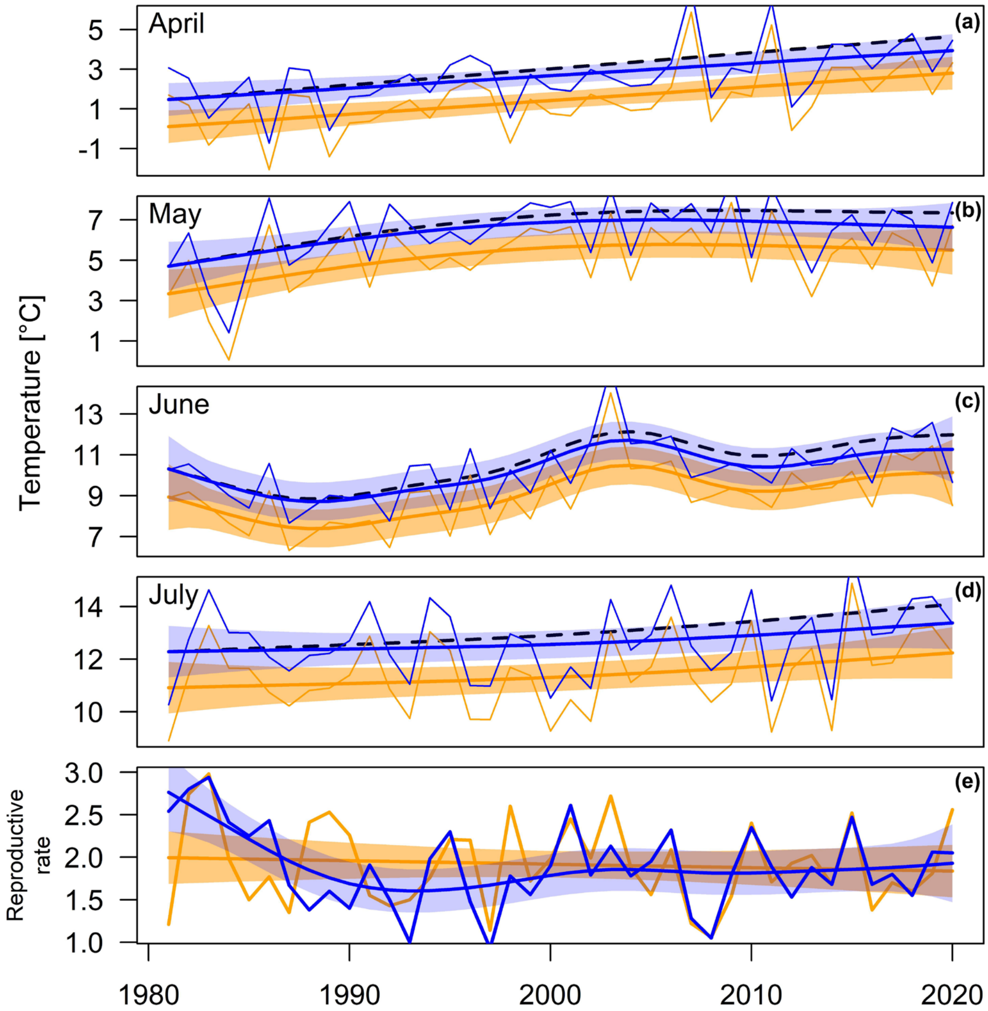

Figure 4. Monthly mean temperature at the average elevation of the black grouse locations (a–d), and reproductive rate (e) in northern Ticino (orange) and central/southern Ticino (blue). The dashed line gives the average temperature development at the average black grouse location of 1981 in central/southern Ticino. The dashed line, thus, gives the temperature hens from central/southern Ticino would have experienced if they did not move upwards, whereas the orange and blue lines show the temperatures hens actually experienced. Shaded areas are 95% uncertainty intervals of the smoothed regression lines.

Brush forest explained the greatest amount of variance (6.2%) in reproductive rate. It showed a curved relationship with an optimum at around 15% cover. Forest, alpine agricultural areas and unproductive vegetation all showed a positive relationship with reproductive rates but the proportion of the variance explained was small.

Year and the interaction between year and region explained a considerable (5.1% and 2.3%, respectively) proportion of the variance in reproductive success. While in northern Ticino reproductive success did not show a negative trend when corrected for weather and habitat changes, there remained a negative trend over the years in central/southern Ticino.

Discussion

Our analysis of 40 years of data on reproductive success of black grouse in the southern Swiss Alps documented relationships between reproductive rates and weather as well as habitat, taking into account changes in distribution of hens. Black grouse hens occurred at higher elevation over the years. Despite the elevational shift they experienced higher temperatures during the breeding period. Reproductive success was positively correlated with temperature and associated with habitat variables. In central/southern Ticino, after correcting for effects of weather and habitat, there remained a negative effect of year on reproductive rates that could not be explained by the variables considered in this study.

Reproductive rate in relation to weather and habitat

The correlation between temperature and reproductive rate showed that high temperatures before and during egg-laying (early June) and early brood-rearing (mid/end of July) were crucial to achieve a high reproductive rate. In our study, hatching date could not be determined directly, but independent

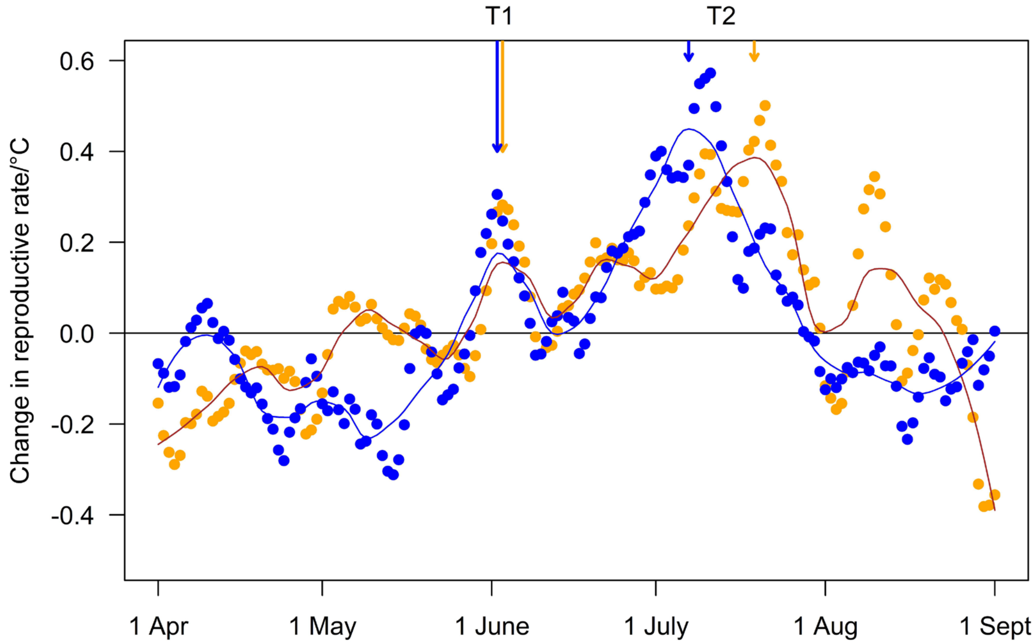

Figure 5. Regression coefficients of reproductive rate on five-day average temperature values for northern Ticino (orange) and central/southern Ticino (blue). Data from all study years pooled. Arrows indicate the critical periods driving reproductive rates, i.e. egg-laying (T1) and early chick-rearing (T2).

data supported the conclusion that the period identified based on the correlation with temperature corresponds to the early brood-rearing period (Pauli 1974, Ellison et al. 1982, Klaus et al. 1990, Rotelli et al. 2021). A positive effect of high temperature on breeding success of grouse was already shown by Naumov 1955 (in Udvardy 1969). Unlike studies in Scotland (Lack 1954, Moss 1986), precipitation did not seem to be important in our study area. The small effect of precipitation could be related to the rainfall pattern typical for the Insubrian climate in the southern Swiss Alps, where in summer most rain falls during thunderstorms. Therefore, even on days with high rainfall dry and sunny periods are often long enough to allow chicks to forage without thermoregulatory stress. Our results indicate that in addition to the conditions during the early hatching period, temperature during the egg-laying period drives breeding success of black

Table 1. Estimated model parameters of the model with reproductive rate as outcome variable and weather and habitat variables as predictors. Given are the standardised coefficients (all variables standardised to a mean of zero and a SD 1), the unstandardised coefficients (all variables measured in the unit given in the last column), the proportion of variance explained in addition to a model that only contains all other variables, and the standard deviation of the variables. The standard deviation of the residuals was 0.22. The variance explained by the overall model was 28% (adjusted R^2). Regions: N-TI = northern Ticino, CS-TI = central/southern Ticino.

Parameter	Standardised coefficient (SE)	Unstandardised coefficient (SE)	Proportion of variance explained (%)	SD of raw data (unit)
Intercept (region N-TI)	2.16 (0.20)	–	–	–
Region (difference N-TI – CS-TI)	−0.36 (0.40)	–	0.2	–
Year (linear trend in N-TI)	−0.04 (0.11)	−0.004 (0.010)	5.1	12 (y)
Year × region (difference in linear trend N-TI – CS-TI)	−0.21 (0.13)	–	2.3	–
Temperature T1	0.11 (0.06)	0.04 (0.02)	3.7	2.7 (°C)
Temperature T2	0.14 (0.07)	0.06 (0.03)	4.3	2.4 (°C)
Precipitation day T1	−0.07 (0.08)	−0.003 (0.003)	0.9	28.5 (mm)
Precipitation day T2	0.13 (0.15)	0.006 (0.006)	0.7	23.9 (mm)
Precipitation night T1	−0.05 (0.07)	−0.002 (0.003)	0.5	28.4 (mm)
Precipitation night T2	−0.15 (0.14)	−0.006 (0.006)	1.0	24.2 (mm)
Alpine agricultural areas	0.16 (0.24)	0.02 (0.04)	0.4	6.7 (%)
Brush forest	1.44 (0.60)	0.40 (0.17)	6.2	3.6 (%)
Brush forest squared	−1.33 (0.52)	−0.01 (0.006)	see brush forest	see brush forest
Unproductive vegetation	0.14 (0.60)	0.05 (0.06)	0.6	3.0 (%)
Forest	0.22 (0.32)	0.03 (0.04)	0.5	7.6 (%)

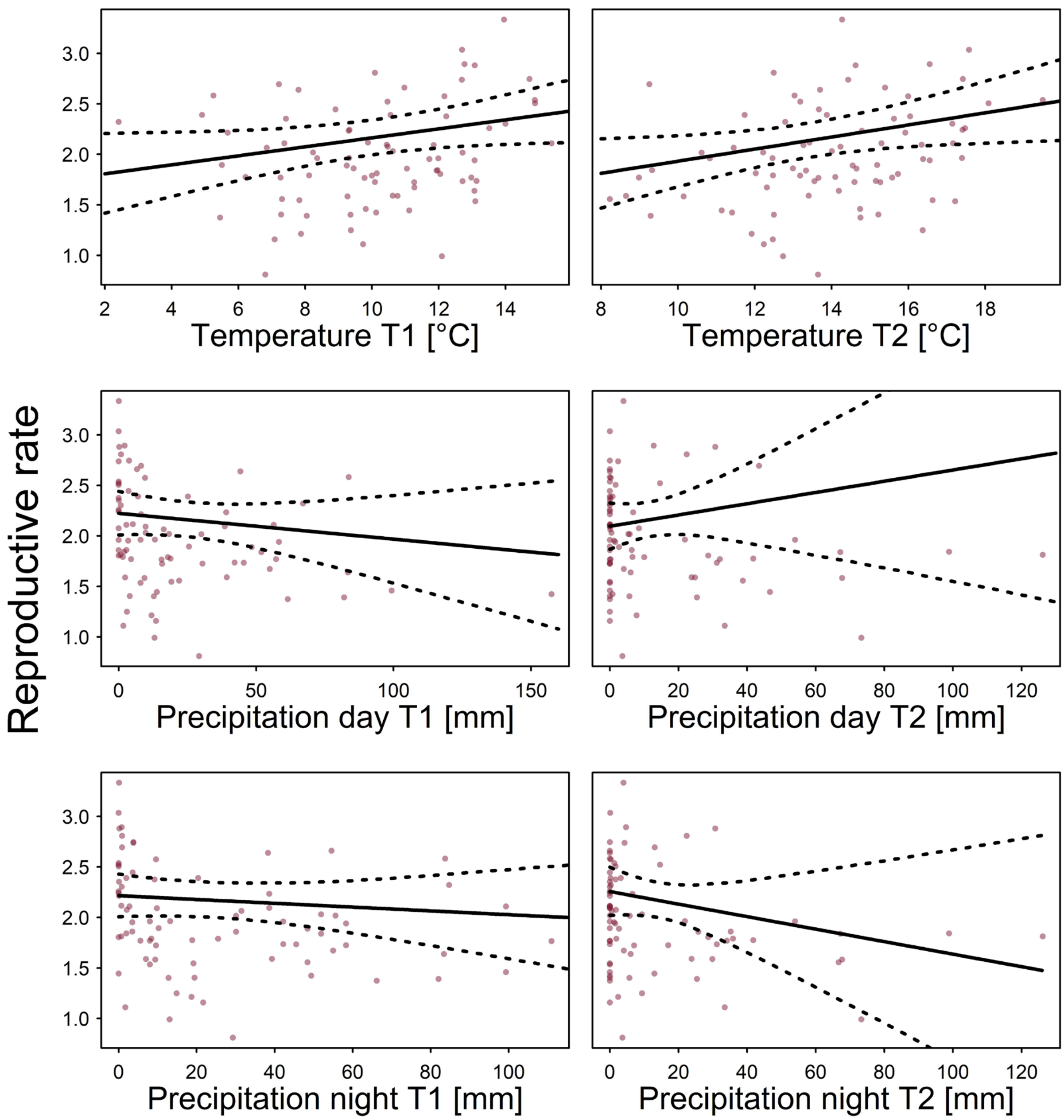

Figure 6. Partial effects of temperature and precipitation during two critical time periods (T1 and T2) on reproductive rates of black grouse.

grouse in Ticino. This pattern compares well with results from studies on several grouse species (Moss and Watson 1984, Brittas 1988, Willebrand 1988, Andreev 1994).

The results of the model indicated that habitat variables, especially the amount of brush forest, were, compared to temperature, of similar importance as drivers of reproductive success. The semi-open landscapes at the upper forest limit are the prime habitat of black grouse in the Alps. In the Swiss Alps brush forest is defined as stands of several low tree and bush species like *Juniperus communis*, *Alnus viridis*, *Pinus mugo* or *Salix* sp. Brush forest is found in naturally disturbed environments, e.g. avalanche runs, but also covers former alpine pastures after land abandonment. The quadratic relationship with reproductive success likely indicated that only the first stages of land abandonment provided suitable habitat for black grouse.

Long-term trends in relation to changes in climate and habitat

Several studies on European grouse species showed changes in phenology, most often an advancement of egg-laying commensurate with increasing spring temperature, although the results were not always conclusive (Moss et al. 2001, Ludwig 2009, Fletcher et al. 2013, Wegge and Rolstad 2017, Ménoni et al. 2020, Coppes et al. 2021). Our data

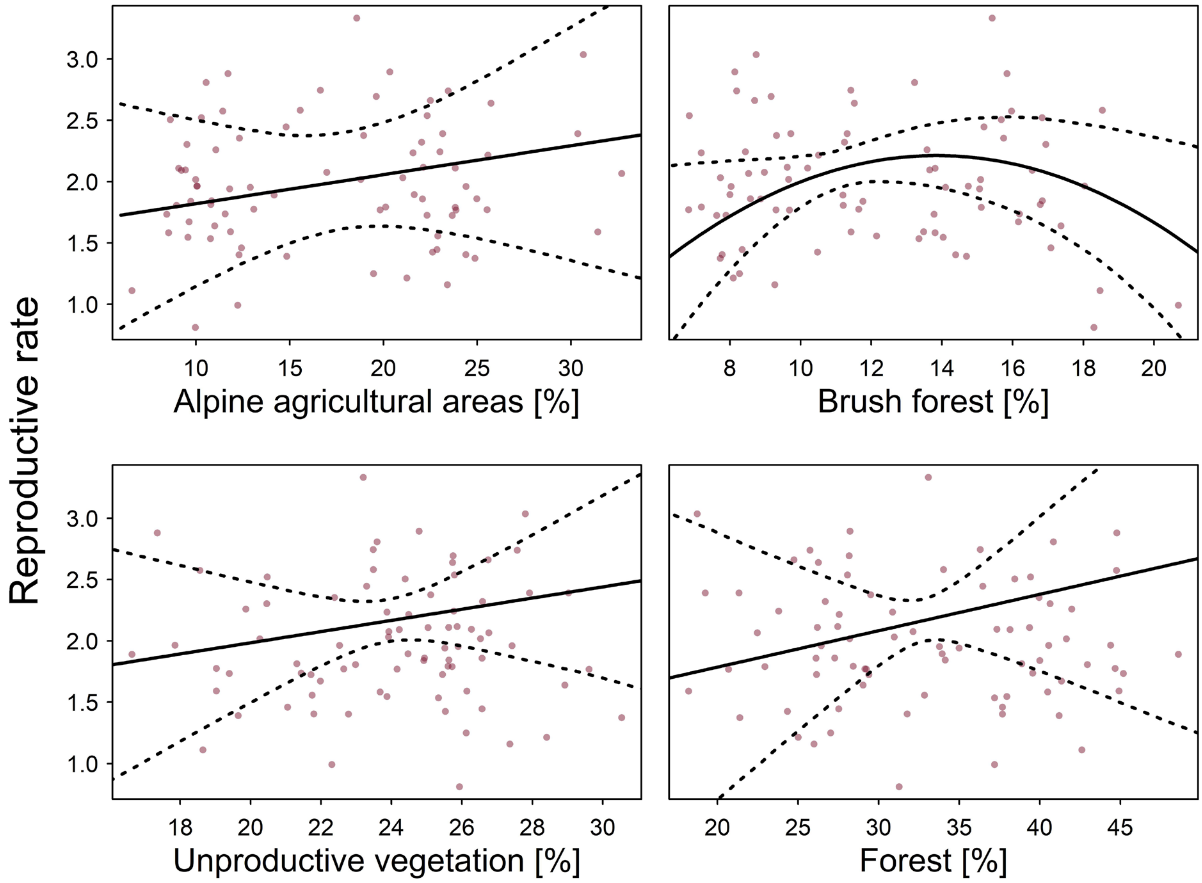

Figure 7. Partial effects of cover by four habitat categories on reproductive rates of black grouse.

did not allow analysing long-term trends in breeding phenology, because precise hatching dates were not known, and the sample sizes were too small to apply the indirect method of determining the egg-laying and early chick-rearing periods separately for early and late study years.

The strong relationship of reproductive success with temperature during the early chick-rearing phase supports previous work in the Italian Alps in an area west of the Ticino with comparable elevations and habitats (Rotelli et al. 2021). The authors combined data from monitoring (spring counts of displaying males and late-summer surveys of hens and chicks) and radio-tracking of black grouse in a seasonal integrated population model to estimate population size and various demographic rates. They found that chick survival was positively affected by ambient temperature in July, and that chick survival in the first weeks was an important driver of the variability in population growth rate. The minimum temperature to achieve a reproductive success sufficient for a stable population is reached in northern Ticino only in the warmest time period of the year, i.e. in July (Zbinden and Salvioni 2004). This pattern may explain the differences in timing of the hatching period between northern and central/southern Ticino. Black grouse appear to hatch later in northern Ticino, which is in accordance with temperature differences related to elevation.

As a consequence of the positive relationship between temperature and reproductive rates we would expect an increase of reproductive output over the study period commensurate with the increasing temperature. However, the model indicated a decline of reproductive rates rather than an increase, although the decline at the beginning of the study period should not be overinterpreted due to the relatively small amount of data in the first years. Whether the decline or lack of an increase is related to a negative effect of climate change to parameters important for black grouse reproduction, remains unclear. Patterns of weather and associated vegetation phenology have changed in the Alps in different ways. Snowmelt advanced on average by 8.9 days over the period 1970–2015 (Klein et al. 2016), and the vegetation growing period started earlier (Studer et al. 2005). In years with early snowmelt, *Vaccinium myrtillus*, an important food plant for black grouse, was accessible earlier but showed a slower subsequent growth (Wipf et al. 2009). Thus, protein-rich food was not necessarily available for black grouse earlier in the season. Average values of variables such as snowmelt or temperature can however be misleading, because marked year-to-year variations in weather conditions are typical for alpine environments. The frequency of years with extreme weather conditions may be more important for long-term trends in reproductive parameters than general climate change, as was indicated in a study of black grouse in the French Alps from 1990 to 2007 (Barnagaud et al. 2011).

The increasing elevations of black grouse breeding sites over time seem counter-intuitive when regarding climatic patterns alone. As indicated by the associations of reproductive success and habitat, changes in habitats are factors to be considered. Land abandonment has led to a decline in alpine agricultural areas. At the elevations used by black grouse these mostly consist of alpine pastures, which gradually have been overgrown by brush forest with increases in tree density at the upper forest limit (Decout 2007, Gehrig-Fasel et al. 2007).

Black grouse reproductive success and elevational shifts in breeding sites were more strongly affected by habitat changes in central/southern Ticino compared to northern Ticino. In the south, forest began encroaching open habitats earlier. The resulting loss of the mosaic of open areas and forest pushed black grouse to higher elevations. The trends in reproductive rates are reflected by a difference in the trends of the number of displaying males counted in the two regions especially in the first part of the study period, with a slight decline in central/southern Ticino and stable but oscillating numbers in the north (Zbinden and Salvioni 2010, Zbinden et al. 2018). In Switzerland generally, black grouse populations declined below 1600 m a.s.l. and increased between 1900 and 2500 m (Knaus et al. 2018).

Conclusion

The results of monitoring reproductive success of black grouse in Ticino over 40 years indicate that reproductive rates are affected by a combination of weather and habitat parameters. Changes in reproductive success over 40 years were limited to the southern region, indicating deteriorating conditions at the edge of the species distribution in the central Alps. Increasing temperatures do not appear to have improved reproductive success, likely as a result of habitat changes that forced black grouse towards higher elevations. The low proportion of variance explained by weather and habitat variables indicates that other factors drive reproductive rates, too. For a non-migratory species, winter conditions are likely to affect the conditions of hens in the subsequent breeding season (Barnagaud et al. 2011). Ski tourism, which has been shown to affect black grouse in other regions of the Alps (Patthey et al. 2008) is not widespread in the Ticino.

Our study and the comparison with the results from northern Europe indicate that the demographic response of grouse populations to environmental changes is complex. Correlations of breeding parameters with coarse proxies of climate change such as mean temperature, and similarly with broad habitat categories, may provide a first indication of possible effects of climate and habitat change. However, more detailed studies to understand the mechanisms leading to changes in breeding parameters and ultimately population trends are necessary as a basis for the conservation of viable populations of black grouse in the Alps.

Acknowledgements – The organisation of the project and data collection were only possible thanks to the collaboration of office staff and gamekeepers from the 'Ufficio della Caccia e della Pesca del Cantone Ticino'. We are particularly thankful to Marco Salvioni, coordinator of the censuses over many years, who unfortunately did not live to see the publication of the results. We thank the hunters who carried out the late-summer counts with their dogs. Luca Rotelli carried out some censuses in southern Ticino for the first years and coordinated data collection in a few years when the first author was absent. Jérôme Guélat, Gabriele Hilke Peter, Samuel Wechsler and Marcel Burkhardt provided technical support for the manuscript.

Funding – Data collection was funded as part of the general tasks of the Cantonal Wildlife Office. The Swiss Ornithological Institute provided in-kind funding to FK.

Author contributions

Niklaus Zbinden: Conceptualization (lead); Data curation (equal); Formal analysis (supporting); Investigation (lead); Methodology (equal); Writing – original draft (equal); Writing – review and editing (supporting). **Fränzi Korner-Nievergelt**: Formal analysis (lead); Visualization (lead); Writing – original draft (equal); Writing – review and editing (equal). **Federico Tettamanti**: Data curation (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Verena Keller**: Conceptualization (equal); Formal analysis (supporting); Visualization (supporting); Writing – original draft (lead); Writing – review and editing (lead).

Data availability statement

Data are available from the Zenodo Digital Repository: <https://doi.org/10.5281/zenodo.5837394> (Zbinden et al. 2022).

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