







ORIGINAL RESEARCH

Using by-catch data from wildlife surveys to quantify climatic parameters and the timing of phenology for plants and animals using camera traps

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Abstract

Gaining a better understanding of global environmental change is an important challenge for conserving biodiversity. Shifts in phenology are an important consequence of environmental change. Measuring phenology of different taxa simultaneously at the same spatial and temporal scale is necessary to study the effects of changes in phenology on ecosystems. Camera traps that take both time-lapse as well as motion-triggered images are increasingly used to study wildlife populations. The by-catch data of these networks of camera traps provide a potential alternative for measuring several climatic and phenological variables. Here, we tested this ability of camera traps, and quantified climatic variables as well as the timing of changes in plant and animal phenology. We obtained data from 193 camera-unit deployments during a year of camera trapping on a peninsula in northern Sweden aimed at studying wildlife. We estimated daily temperature at noon and snow cover using recordings provided by cameras. Estimates of snow cover were accurate, but temperature estimates were higher compared with a local weather station. Furthermore, we were able to identify the timing of leaf emergence and senescence for birches (*Betula* sp.) and the presence of bilberry berries (*Vaccinium myrtillus*), as important food sources for herbivores. These were linked to the timing of the growth of antlers and the presence of new-born young for three ungulate species as well as the presence of migratory Eurasian cranes (*Grus grus*). We also identified the timing of spring and autumn moulting of mountain hares (*Lepus timidus*) in relation to snow cover. In this novel study, we show the potential of (by-catch) data from camera traps to study phenology across a broad range of taxa, suggesting that a global network of camera traps has great potential to simultaneously track wildlife populations and the phenology of interactions between animals and plants.

Introduction

Better understanding global environmental change is a prerequisite if we want to conserve the world's biodiversity. One important consequence of environmental change is a shifting of phenology (the seasonal timing of biological events), which can have major effects on ecosystems, for example, when the phenology of interacting species

shifts differently resulting in mistiming (Root et al. 2003; Visser and Both 2005). Phenological studies differ in the spatial scales at which data are collected, such as remote-sensing satellites (large scale) or observational plots (small scale), making it difficult to compare studies as measurements of the same phenomenon from different spatial scales do not always show consistent patterns and variability among different scales are not yet well understood

(Badeck et al. 2004). Furthermore, different methodologies often make it challenging to integrate data from multiple taxa (Morissette et al. 2009). Thus, there is an opportunity and need to measure both climatic and phenological timing data for a range of taxa at the same spatial and temporal scale.

Recently, there has been an increase in the use of digital cameras to monitor plant phenology, for which the term 'phenocam' is now generally used (Richardson et al. 2009; Brown et al. 2016). These phenocams take time-lapse images which can be used to study a range of phenophases such as leaf emergence and senescence, and flowering (Brown et al. 2016; Alberton et al. 2017). A station deploying external sensors with a phenocam enables the linkage of the camera images to climatic measurements such as temperature at the same spatial and temporal scale (Brown et al. 2016). Therefore, phenocams could provide a single station that can measure both climatic data, structural changes in the landscape (flooding, deforestation, fire events etc.) and phenological timing for a range of taxa and produce spatial and temporal coverage of trends, which might otherwise be much more expensive to obtain. They, however, typically lack an active trigger activating the camera. This may be problematic when studying animal species or populations that occur at low densities, which significantly reduces the probability of detecting species with fixed interval time-lapse photography, especially when time intervals larger than 5 min are used (Hamel et al. 2013).

Camera traps are (digital) cameras that mostly use a passive infra-red (PIR) sensor to detect moving animals (Welbourne et al. 2016), although the term 'camera trap' has also been used for time-lapse cameras (Meek et al. 2014). While PIR-sensor triggered camera traps are mainly used to detect the presence of large mammals, they are increasingly being used for a broad range of applications (Burton et al. 2015), including studying migration phenology (e.g. Jachowski et al. 2015). Most of the commercially available models used in these studies also have the possibility to take time-lapse images (Rovero et al. 2013), which are often used to test camera functioning, but not for image-analysis related to ecological questions (but see Sirén et al. 2018). The advantage of a PIR-sensor triggered camera trap over a phenocam taking time-lapse images is that rare events, such as animals at low densities moving past the camera, can be recorded (Hamel et al. 2013). Furthermore, most of the commercially available models can also measure temperature (Rovero et al. 2013), although care has to be taken about the usability of these data (Sirén et al. 2018). Thus, camera traps provide the opportunity to study plant phenology and climatic variables, and relate these to the phenology of animals at low densities at the same spot

simultaneously through a single device. Such measurements from a single device can then be combined with satellite data to predict patterns over larger geographical scales (Richardson et al. 2018; Sirén et al. 2018).

In this study, we used by-catch data from a camera trap survey investigating mammal-community composition to quantify midday temperature, snow cover and the timing of phenological events for plants and animals. We performed 1 year of camera trapping in a boreal forest system in northern Sweden. Using an array of metrics, we aimed to demonstrate the broad applicability of by-catch data from camera traps to link local climatic data and plant phenological transitions to animal phenological events sensitive to potential phenological mismatches (Visser and Both 2005; Post et al. 2008; Plard et al. 2014). Such use of camera trap by-catch data could greatly advance the study of phenology of interactions between plants and animals. Specifically, as a proof-of-concept, we focussed on (1) climatic variables related to camouflage of species that turn white in winter (Mills et al. 2013) and (2) the phenology of important food-plant species for herbivores (Hjeljord et al. 1990; Post and Stenseth 1999; Wam et al. 2017) and (3) link these to animal phenology related to fitness, namely onset of moult, calving date and growth of antlers (Linnell and Andersen 1998; Price et al. 2005; Mills et al. 2013).

Materials and Methods

Study system and camera trapping design

The study site is located on Järnåshalvön, a c. 200-km² peninsula in the Baltic Sea in northern Sweden (63° 32' N, 19° 41' E), characterized by a relatively flat topography and a mixture of boreal forest, mires and agricultural land. Our study design consisted of 11 rectangular transects of 4 km evenly distributed over the peninsula as described by Pfeffer et al. (2018). On each transect, we selected 18 locations with a regular spacing of 100 m between locations to deploy the camera traps (Fig. S1). Our set-up was designed to study mammal community composition on the peninsula. We sampled a total of 198 locations from 29 January 2017 until 14 February 2018, however, due to malfunction of cameras (2), a fallen tree (1) and wrong placement of cameras (2), the total number of locations used in the analysis was 193 (Fig. S1). At the start of the project, we placed three camera traps with IR-flash (HC500, RECONYX Inc., Holmen, WI) on trees along each transect with a minimum distance of 200 m between cameras. After 6–10 weeks we moved these camera traps to new locations on the same transect, while swapping SD-cards and batteries. We moved the cameras six times to cover all locations.

At each predefined location, we selected the tree nearest our GPS point (<40 m, but most were within 10 m) that had a good visibility towards the north and placed the camera traps 60 cm above the ground or top of the snow. We placed cameras to face north to reduce false triggers and unidentifiable pictures due to direct sunlight and we placed cameras with a field of view parallel to the ground to increase the detection probability for a whole range of species (Hofmeester et al. 2017). We set the cameras to take a time-lapse image at noon every day to check camera functioning. Additionally, to track animal presence, we set the cameras to take a series of ten photographs when triggered by the PIR-sensor with no delay before the initiation of the next sequence, and we set the PIR-sensor to the highest sensitivity. Our final dataset contained 193 deployments, with a sampling effort of 10 491 camera-trap days spread over a period of 382 days.

Abiotic factors and plant phenology

We used the time-lapse images, that were initially taken only to check camera functioning, to estimate temperature and snow cover as climatic variables (Fig. 1A), and important plant phenological changes related to food availability for animals: leaf emergence and senescence of birches (*Betula pendula* and *Betula pubescens*) and the presence of bilberry berries (*Vaccinium myrtillus*; Fig. 1B). We first went through all images to classify temperature, snow cover and the functioning of the camera. If the camera's point of view had shifted from previous images, for example due to the fact that the camera was not properly mounted on the tree, we did not consider any further images from that camera. Similarly, we did not consider images during days when the time-lapse image was completely white, grey or black, most probably due



Figure 1. Example images to show phenophases. (A) Time-lapse image showing 100% snow cover and a temperature of -22°C . (B) Time-lapse image showing the presence of coloured leaves on birches (*Betula pendula* and *Betula pubescens*) and the presence of ripe fruit on lingonberry (*Vaccinium vitis-idaea*). (C) Sensor-triggered image showing a mountain hare (*Lepus timidus*) moulting with 51–90% white coat in a fully green (0% white) landscape. (D) Sensor-triggered image showing a Eurasian moose (*Alces alces*) with growing antlers.

to snowfall covering the camera lens or ice forming on the lens in cold conditions. For all other images, we noted the temperature recorded by the camera and visually estimated the percentage snow cover in the lower half of the image (Fig. 1A). We estimated snow cover as the percentage ground that could not be seen due to snow, which corresponded to a snow layer of approximately 5–10 cm thick. To reduce classification error, we decided to group classifications into four intervals: 0–10%, 11–50%, 51–90% and 91–100%. Due to insufficient records per transect for the animal phenology and our intention to get comparable estimates of phenology for multiple taxa, we combined data from all camera locations to determine averages for the whole study area. We calculated daily averages for temperature at noon (from here on referred to as midday temperature) and snow cover.

We retrieved data from the Swedish Meteorological and Hydrological Institute website (www.smhi.se) for the Järnasklubb weather station (63°26'09.2"N, 19°40'36.5"E) for temperature and the Torrböle weather station (63°42'27.4"N, 19°35'35.5"E) for snow depth (Fig. S1), as both weather stations only recorded one parameter of interest, and used these data to check the reliability of the temperature and snow cover data from the cameras. We transformed snow depth data into snow cover data as follows: when snow depth was zero, we noted this as a snow cover of zero, when snow depth was 0–5 cm, we recorded it as 50% snow cover; all snow depths above 5 cm were considered 100% snow cover.

In a second round, we went through the selected images, to classify plant phenophases. We divided plant phenophases into two groups: vegetative and reproductive phenophases (Table 1). Specifically, we looked at the presence of leaves (both new and mature leaves), coloured leaves (still attached) or falling leaves (as identified by leaves on the ground or clear visible gaps without leaves on branches) for broadleaved trees and shrubs (vegetative phenophases), and for the presence of flower buds, open flowers, berries or ripe berries (reproductive

phenophases). We considered the whole image when classifying trees and shrubs, whereas only the lower 1/3rd of the image was considered for the herbaceous layer.

To speed up the classification of plant phenophases, we grouped images per week and recorded if specific phenophases were present during that week. In practise, this meant that we checked several images in a week, including the first and the last image, for the presence of a phenophase. If the phenophase was present in any of the checked images, that week was classified as having the phenophase present, if none of the checked images contained a certain phenophase, that phenophase was considered absent in that week. This meant that we classified a gradual process as presence/absence to decrease the potential for classification errors, which resulted in a dataset with presence/absence at a camera trap site in a temporal interval of 1 week. We then summarized this information for the whole study area by calculating the ratio of sites with a phenophase present over all sites with an active camera trap per week. We did this to capture the temporal trends in the onset of phenophases.

Animal phenology

We used the sensor-triggered images to measure animal phenology. Here we focussed on four parameters: (1) the change of coat colour of mountain hare (*Lepus timidus*) that have a white winter coat and brown summer coat (Fig. 1C), (2) antler growth of three ungulate species (Fig. 1D), (3) the presence of new-born young of three ungulate species and (4) the timing of arrival and departure of migratory Eurasian crane (*Grus grus*). We first went through all the images to check if there was an animal in the frame. Images were automatically put into sequences based on timing, where images taken within a period of five minutes were grouped into a single sequence or event. We removed all images without animals from the database. For each sequence with an animal, we recorded the species, number of animals, and where visible from the images (depending on image quality and species), the sex and age (juvenile or adult).

From this first classification, we made subsets of sequences for the different phenophases: presence of migratory species, presence of juveniles, presence of summer/winter coat and the growth of antlers (Table 1). For the presence of summer/winter coat, we selected all mountain hare sequences to quantify 'the whiteness of the coat of mountain hares'. Coat whiteness was set to 100% for full winter coat and 0% for full summer coat. During the time when hares were moulting, whiteness was estimated visually in intervals of 0–10, 11–50, 51–90 and 91–100% (see Fig. S2). We used all images in a sequence of a passing mountain hare to estimate the

Table 1. Animal and plant phenophases used in this research. All phenophases are described in the standardized phenology monitoring method as reported by Denny et al. (2014) except the growth of antlers

Animal	Plant	
	Vegetative phenophases	Reproductive phenophases
Presence of migrating species	Coloured leaves	Flowers or flower buds
Presence of juveniles	Falling leaves	Open flowers
Summer coat/Winter coat	Leaves	Fruits
Growth of antlers		Ripe fruits

whiteness of the coat to get as good an estimate as possible. We then calculated weekly averages based on the mean or extreme value to represent each class: 0 for 0–10%, 30 for 10–50%, 70 for 51–90% and 100 for 90–100%, for both the whiteness of the mountain hare coat and snow cover to match the two parameters.

We selected all ungulate sequences to check for the presence of antlers. We classified antlers as ‘growing antlers’ when there was still skin and fur (velvet) around the antlers. We used the first appearance of growing antlers as an estimate of the timing of the onset of antler growth, whereas the timing of transition from growing antlers to mature antlers gives an estimate of the timing of antler maturation or hardening.

We selected all ungulate sequences where juveniles were classified in the initial classification to determine the first appearance of new-born young for the three ungulate species. This timing is used as a measure of the timing of calving, which is again an important phenophase with high-energy demand that could be linked to plant phenology (Linnell and Andersen 1998). We used the first and last appearance of cranes in front of our camera traps as an estimate of the timing of migration.

All classifications were performed by one person (either TH or SY) after which a subset (approximately 20%) were checked by TH to ensure consistent classification between observers.

Statistical analysis

All analyses were performed in R Studio 1.0.153 running R version 3.6.0 (RStudio Team, 2016; R Core Team, 2019). We used change-point or breakpoint analysis to estimate the timing of changes in abiotic factors and phenology as implemented in the *strucchange* package (Zeileis et al. 2002, 2003). We modelled the parameter of interest as a function of time to identify points where mean and slope change as an indication of changes in abiotic factors or the onset of phenological phases. We used time series with average estimates per day (temperature and snow cover) or week (phenology) for the analysis, and used Bayesian Information Criterion (BIC) values to select the number of breakpoints identified. We selected the number of breakpoints based on the model with the lowest number of breakpoints (Zeileis et al. 2003), except for the presence of leaves on birch and the presence of berries on bilberry, where visual inspection of the data showed that one of the identified breakpoints was in a place where no visible change occurred. In these cases, we selected the model with one breakpoint less, which was always within $\Delta\text{BIC} < 4$ compared to the model with the lowest BIC value, suggesting comparable model fit (Burnham and Anderson 2004). We represent the identified breakpoints

and their 95% confidence intervals (CIs) unless these were too small to identify given the temporal resolution of our data, in which case only the estimate of the breakpoint is given.

We had missing data for the whiteness of mountain hares for 5 weeks (9% of data points) because we did not observe any mountain hares during these weeks. As breakpoint analysis using the *strucchange* package cannot handle missing data, we used the average for the week before and after the missing value to estimate the whiteness of mountain hares in these weeks. As all missing values were outside the main periods of change, we thus assumed that animal coat colour did not considerably change outside those periods. As week numbers may be hard to interpret, we also present results from analyses based on week numbers as the date of the Thursday in that week (which is the mid between Monday and Sunday).

We calculated the Pearson correlation coefficient to check how well our measurements of temperature and snow cover corresponded to the weather station data. After that, we checked for differences between weather-station and camera-trap derived temperatures using a linear mixed model with a random intercept per date. We did this for the whole dataset, as well as for subsets using the periods between breakpoints as identified by our analysis, to check if potential biases in camera-derived temperatures were different between the seasons. We performed a more detailed analysis on the temperature data where we tested for the effect of distance to the coast on camera-trap derived temperature measurements, which we present in Data S1.

Results

Abiotic factors

We obtained daily estimates of abiotic factors for 382 days from 29 January 2017 until 14 February 2018. Average midday temperature as measured by camera traps showed a pattern consistent with the nearby Järnasklubb weather station ($r = 0.95$) although camera traps consistently recorded higher temperatures (β : 1.9°C, t -value: 11.77, d.f.: 381, $P < 0.001$; Fig. 2A). We recorded temperatures below 0°C prior to 9 March and after 30 October and identified three breakpoints in temperature, on 19 May (95% CI: 12–22 May), 26 July (95% CI: 25–27 July) and 13 November (95% CI: 3–14 November) splitting our study time into four periods (Fig. 2A). The bias in camera-trap recorded temperatures varied between seasons. Cameras recorded higher temperatures than the weather station before 19 May 2017 (β : 3.2°C, t -value: 15.99, d.f.: 110, $P < 0.001$) between 19 May and 26 July (β : 4.9°C, t -value: 18.61, d.f.: 67, $P < 0.001$) and between

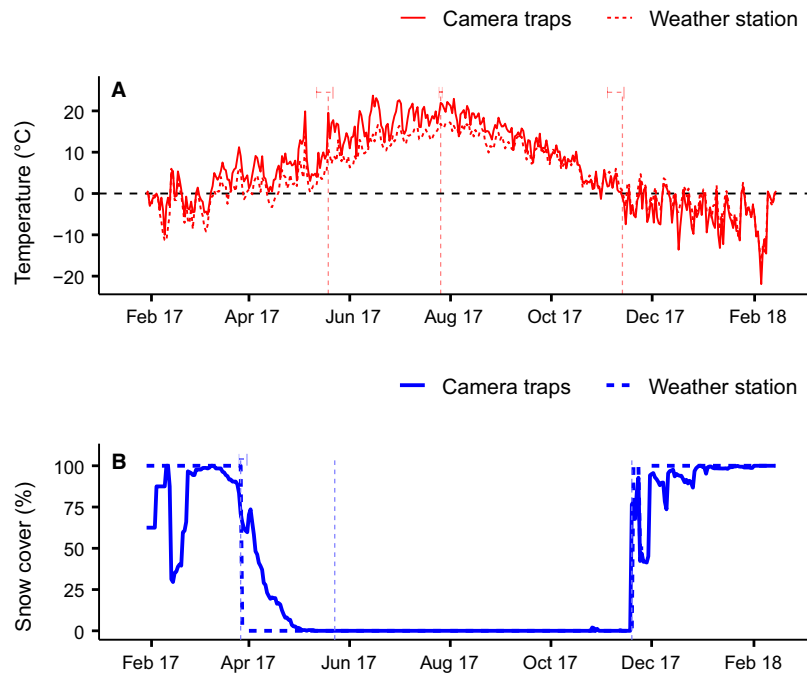


Figure 2. Estimates of (A) average daily temperature and (B) percentage of snow cover obtained using time-lapse images of camera traps. Solid line shows the midday averages as derived from camera traps, the dashed line shows the daily averages as derived from the weather stations at Järnäsclubb and Torrböle, respectively. Vertical dashed lines indicate identified breakpoints and their 95% confidence intervals.

26 July and 13 November (β : 1.7°C , t -value: 8.29, d.f.: 109, $P < 0.001$). The pattern switched after 13 November, when cameras recorded lower temperatures than the weather station (β : -1.7°C , t -value: -7.89 , d.f.: 92, $P < 0.001$). There was no consistent pattern in temperature as a function of the distance of a camera trap from the coast (Data S1).

Snow cover occurred prior to 11 May and after 25 October, which was consistent with the pattern of the nearby weather station ($r = 0.94$; Fig. 2B). We again identified three breakpoints, on 27 March (95% CI: 26–31 March), 23 May and 19 November, which corresponded to the onset of snowmelt, the disappearance of snow and the start of continuous snow cover (Fig. 2B). The onset of snowmelt occurred 18 days after the last midday temperature below 0°C , whereas the disappearance of snow coincided with the breakpoint in temperature around 20 May, when midday temperatures were above 10°C .

Plant phenology

We obtained weekly estimates of plant phenology for 53 weeks from 13 February 2017 until 14 February 2018. Although we classified all plants in view, we only present results for birches and bilberry as these species were present in most locations, had phenophases that were easy to recognize and showed clear seasonality.

The first birch leaves appeared in week 20 (around 18 May; Fig. 3A). We identified two breakpoints for the presence of green leaves: leaf emergence in week 22, around 1 June (95% CI: 21–23) and the disappearance of green leaves in week 35, around 31 August (95% CI: 34–36; Fig. 3A). The first break point is 1 week later than the identified breakpoint for the disappearance of snow. The second break point coincided with the appearance of coloured leaves, for which two breakpoints were identified in week 35 (95% CI: 33–36) and week 42, around 19 October. We identified the same breakpoints for falling leaves in week 35 and 42 (95% CI: 41–44; Fig. 3A). All birches had lost their leaves by week 43, around 26 October.

The bilberry berries appeared in week 30 (around 27 July; Fig. 3B). We identified three breakpoints for the presence of bilberries, the appearance of bilberries in week 31, around 3 August (95% CI: 30–32), a start of a decline in the presence of berries in week 38, around 21 September (95% CI: 37–40) and the disappearance of berries in week 45, around 9 November (95% CI: 44–46).

Animal phenology

In total, we obtained 176 passages of mountain hares in which we could determine the whiteness of the coat during 52 weeks from 15 February 2017 to 11 February 2018. When analysing snow cover on a weekly scale, we

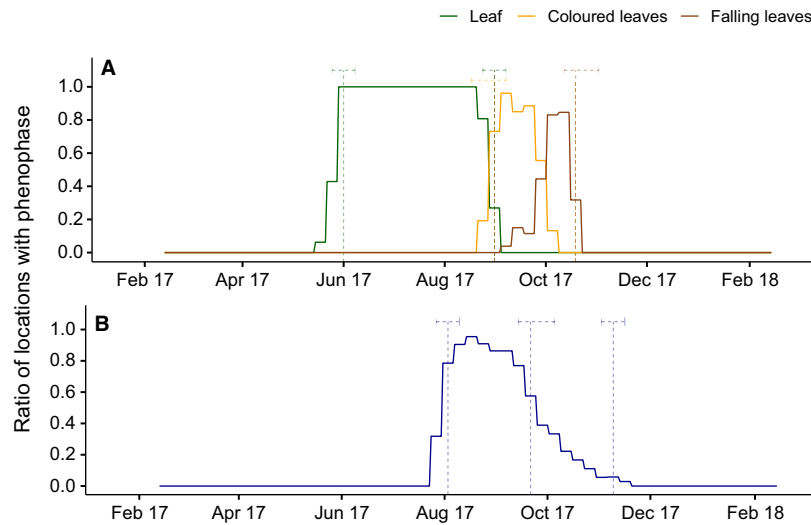


Figure 3. Timing of (A) the presence of leaves (green), coloured leaves (yellow) and falling leaves (brown) for birches (*Betula pendula* and *Betula pubescens*) and (B) the presence of berries for bilberry (*Vaccinium myrtillus*) as obtained using time-lapse images of camera traps. Solid line shows the weekly ratio of sites where the phenophase was observed, vertical dashed lines indicate identified breakpoints and their 95% confidence intervals.

identified three breakpoints in week 14, around 6 April (95% CI: 13–21), week 21, around 25 May (95% CI: 20–23) and week 47, around 23 November (95% CI: 46–48; Fig. 4). In contrast, we identified four breakpoints for the coat colour of mountain hares, resulting from the difference between a gradual biological process (moulting of mountain hares) resulting in two break points in both seasons and a gradual (melting of snow in spring) and spontaneous environmental process (the first snow fall) resulting in only one break point in autumn. The identified break points for hares coincided with the onset of the spring moult in week 15 (around 13 April), the end of the spring moult in week 22 (around 1 June), the onset of the autumn moult in week 40 (around 5 October) and

the end of the autumn moult in week 47 (around 23 November; Fig. 4). We thus identified a period of mismatch of 7 weeks in autumn (week 40–47) in which mountain hares were already turning white while there was no snow. The worst mismatch happened between the first record of a moulting hare that was >50% white on 8 November and the first snowfall on 25 November, a period of 17 days. We recorded the first fully white hares in the same week as the first snowfall (week 47).

We obtained 636 passages of roe deer, 482 passages of red deer and 248 passages of moose from 31 January 2017 until 4 January 2018. Growing antlers were noted on 21 passages of roe deer, 6 of red deer and 13 of moose. The first and last date at which growing antlers

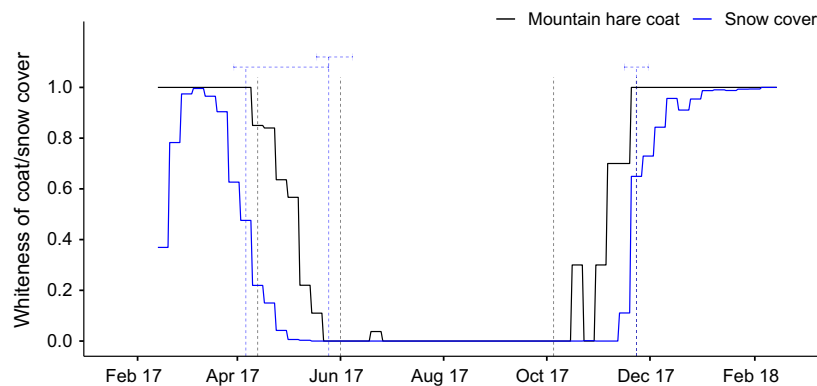


Figure 4. Estimates of snow cover (blue) and the coat colour (black) of mountain hares (*Lepus timidus*) as obtained using camera traps, where 1 shows a completely white hare or 100% snow cover. Solid lines show weekly averages, vertical dashed lines indicate identified breakpoints and their 95% confidence intervals.

were observed per species are given in Table 2. Our records suggest a difference between the species in timing of antler growth, where roe deer showed the earliest and moose the latest period in which growing antlers were observed. We recorded new-born young in 11 passages of roe deer, 15 of red deer and 10 of moose. The date at which the first new-born young was observed per species are given in Table 2. Here, red deer showed the earliest and moose the latest date on which the first young was observed. When comparing observations of new-born young with the leaf emergence of birch (as an indication of food availability), we see that the first observations of new-born roe deer coincide exactly with the timing of leaf emergence, whereas new-born moose were observed 1 week after leaf emergence. New-born red deer, in contrast, were observed 2 weeks prior to leaf emergence when there was still some remaining snow on the ground.

We obtained 33 passages of Eurasian cranes. The first passage, of a pair of adult birds, was on 16 June. The last passage was on 18 August and showed an adult pair with a fully grown juvenile. These dates fall fully within the period in which birch had green leaves and after the snow had disappeared.

Discussion

Simultaneously measuring changes in phenology for a large range of taxa is important to study the effects of environmental change on ecosystems. Here, we tested the potential of using by-catch data from camera trap studies aimed at wildlife to measure climatic variables as well as the timing of changes in plant and animal phenology. We obtained site-level estimates for animal phenophases and related these to two climatic parameters and plant phenological transitions using a year of camera trapping data from northern Sweden, enabling the quantification of relations among different groups of taxa (Fig. 5).

Although our camera-trap derived midday temperatures showed a similar seasonal pattern compared to a nearby weather station, we found that camera-derived

temperatures were biased in all seasons. These biases could be the result of methodological factors, environmental differences or inaccuracy of the temperature sensor in the camera traps. Biases were not related to the distance to the coast (Data S1), but could be related to differences in local habitat and topography, as well as low accuracy of the temperature logger in the used camera traps. As the cameras did not have solar radiation shields, this might have resulted in higher temperature measurements, especially in summer (Meek et al. 2014; Sirén et al. 2018). Combining camera traps with external temperature loggers would reduce this issue (Sirén et al. 2018). Although our estimates of midday temperature were biased, they did show the same temporal pattern as data obtained from the weather station, which suggests that data from multiple study sites using the same camera type could be used as a covariate studying differences in animal phenology at these sites. However, further investigation of the effect of methodological and environmental features on camera-derived temperature measurements are needed if these measurements are to be used for site-specific inferences of temperature related to phenology.

We focused our analysis on three plant species, birches (*Betula pendula* and *Betula pubescens*) and bilberry (*Vaccinium myrtillus*) that are important food species for ungulates (Hjeljord et al. 1990; Post and Stenseth 1999; Wam et al. 2017). These species were relatively easy to study as they have clear seasonality and visually identifiable phenophases at the resolution of our camera-trap images. Other important food items for herbivores, such as herbaceous species, became available during green-up after snowmelt, which coincided with the leaf emergence in birches. The timing of berry production of bilberries could be used as a measure of food availability for, for example, brown bears (*Ursus arctos*; Nijland et al. 2013; Hertel et al. 2016). As such, we conclude that camera traps can be used to study phenological transitions in food plants for herbivores, enabling the comparison of herbivore phenology with food phenology.

We quantified the camouflage of mountain hares (*Lepus timidus*) using camera traps and identified a mismatch between coat colour and snow cover during the autumn moult. Our results show a similar pattern to that which was found for the related snowshoe hare (*Lepus americanus*; Mills et al. 2013). To our knowledge, we are the first to show such a pattern for mountain hares. Such a mismatch might potentially be problematic as animals with the wrong coat colour have an increased chance of being predated (Mills et al. 2018). This calls for further research on the timing of moult and potential camouflage mismatch in the mountain hare as previous studies indicated that this mismatch might contribute to the ongoing decline in mountain hares in Scandinavia (e.g. Pedersen et al. 2017).

Table 2. Timing of phenology for the different phenophases. Dates are based on first and last record by the camera traps except for new-born young, in which case only the first dates are reported

Phenophase	First	Last
Presence of growing antlers: Moose	31 May	19 August
Presence of growing antlers: Red deer	8 May	24 July
Presence of growing antlers: Roe deer	20 February	27 May
Presence of new-born young: Moose	7 June	
Presence of new-born young: Red deer	20 May	
Presence of new-born young: Roe deer	3 June	
Presence of Eurasian cranes	16 June	18 August

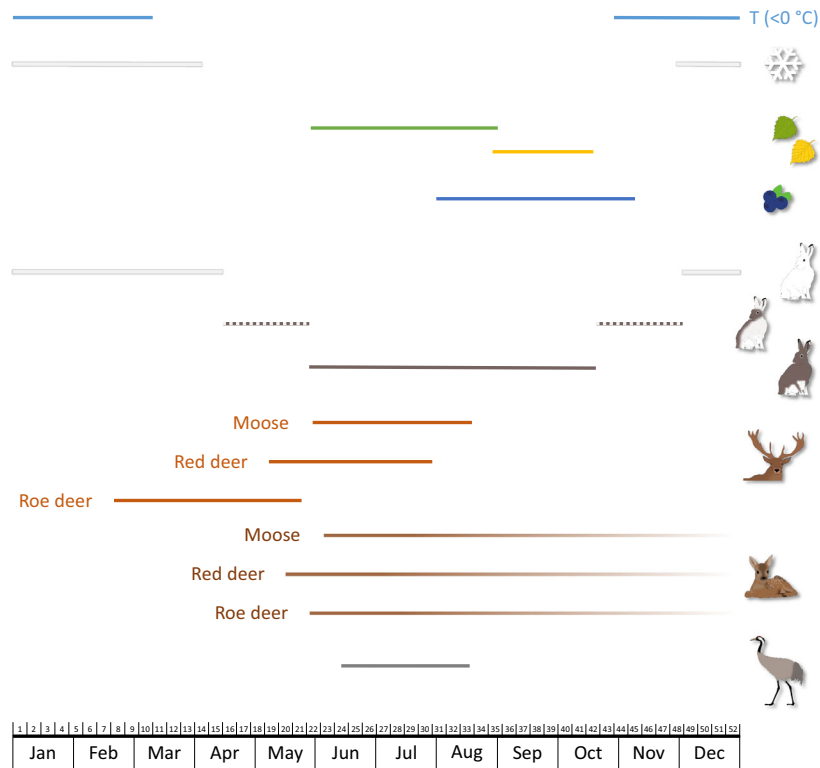


Figure 5. Overview image showing the timing of climatic and phenological events for all taxa enabling the comparison between different taxonomic groups. The different symbols represent the different taxonomic groups and timing is given by week number based on the findings in this study.

There was a clear difference in antler hardening phenology between roe deer, and the other two cervids, which reflects the very different life-history cycle of roe deer, which have the rutting season in summer, compared to autumn for the other species (Liberg et al. 1998; Melis et al. 2005; Hoem et al. 2007). Although we did not have enough images to test it here, it should be possible to quantify the date of antler casting in autumn-winter as well. The dates on which new-born young were seen showed some variation, which reflects the biology of the studied cervids. All three species are known to reduce movement and seek out secluded areas in the period immediately following birth in order to reduce the exposure of their young to predators and inclement weather (Espmark and Langvatn 1985; Linnell et al. 1998; Bowyer et al. 1999). These behaviours will generally reduce the visibility of young during the first weeks-months of life. This is reflected in the first observations for roe deer being somewhat later than the expected birth data for Scandinavia (Linnell and Andersen 1998). Although our sample size was limited, we think that camera traps show great potential for the estimation of the timing of reproduction in cervids, and for the estimation of the mean number of young per female in polytocous species such as roe deer and moose. One advantage of studying

the status of animals that are detected (antler or moult status), is that it circumvents problems related to detection of animals by camera traps (reviewed by Hofmeester et al. 2019) assuming that the detection does not change with the status of the animal. However, several estimates of animal phenology, such as detecting juveniles and the mean number of young per female, do suffer from imperfect detection of camera traps, and as such, methods need to be developed to correct for potential detection biases.

We found a clear link between measured temperatures and snowmelt, snowmelt and leaf emergence of birch, and leaf emergence of birch and reproduction of cervids. The latter showed a slight mismatch between reproduction of red deer and plant phenology, where red deer fawns were born before the leaf emergence of birch. This mismatch could be a result of the relatively recent establishment of this species in our study area at the northern edge of its distribution (Milner et al. 2006). As the duration of snow cover has decreased and the length of the growing season increased in Sweden in recent years (data available from www.smhi.se) the date for leaf emergence is likely to become earlier, reducing the mismatch for red deer, but potentially increasing the mismatch for roe deer and moose (Plard et al. 2014).

There were several limitations of our by-catch data compared to the regular use of phenocams for plant phenology (Brown et al. 2016). First of all, we moved our cameras throughout the season, a common practise in wildlife studies to increase sample size with a limited number of cameras (Burton et al. 2015). This, however, meant that we could never determine all shifts in phenophases at a single site. Due to generally low detection rates of animals, studies of animal phenology using camera traps will most likely need to average across cameras to obtain estimates at the level of study sites. Therefore, site-averaged estimates of plant phenology to link to animal phenology should be useful in such studies. However, when plant phenology is the main aim of the study, it is not advised to move cameras during the period of interest. Second, we only took one image a day at noon, whereas phenocams are often set to take multiple pictures a day, a method known as ‘repeat photography’ (Sonnenntag et al. 2012). This could easily be solved by setting camera traps to take multiple time-lapse images a day for the specific purpose of getting a higher temporal resolution for environmental and phenological data. Third, we never placed the cameras close to plants or aimed at the canopy, which is common practise with phenocams (Brown et al. 2016), as that would reduce the probability of capturing animals. This reduces the possibility to use automated colour analysis as it is harder to have a large enough part of the picture covered by the species of interest (Sonnenntag et al. 2012). Automated colour analysis of camera trap images is possible if the species of interest covers a large enough proportion of the frame and the camera has a fixed white balance (as the cameras we used), which enables extraction of comparable RGB values from images taken during differing light conditions (Sonnenntag et al. 2012). We suggest that future efforts investigate the usability of by-catch data from camera traps for automatic classification of plant phenology using methods already developed for phenocams (e.g. Sonnenntag et al. 2012).

Overall, we think that by-catch data from camera traps used to study wildlife populations show a great potential to study animal phenology and associated abiotic and plant phenological transitions, that is the phenology of interactions between plants and animals. Calls for a global network of phenocams (Brown et al. 2016) and camera traps (Steenweg et al. 2017) can thus be merged into one network if proper standardization can be obtained for both the study of plant and animal phenology and changes in animal abundance. In addition, we show that much information can be retrieved from time-lapse images initially taken only to check camera functioning. With this in mind, it is becoming increasingly important to use meta-data standards and a good infrastructure to

store camera trap images to make these by-catch data usable (Bubnicki et al. 2016; Forrester et al. 2016) and to further develop automatized ways of analysing phenology from camera trap images (Sonnenntag et al. 2012).

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Conflict of Interest

The authors declare no conflict of interests.

Data Accessibility

All data underlying the analyses are presented in Datas S2 and S3. Raw camera trap images can be acquired from the corresponding author upon reasonable request.

References

- Alberton, B., R. D. Torres, L. F. Cancian, B.D. Borges, J. Almeida, G. C. Mariano, et al. 2017. Introducing digital cameras to monitor plant phenology in the tropics: applications for conservation. *Perspect. Ecol. Conserv.* **15**, 82–90.
- Badeck, F.-W., A. Bondeau, K. Böttcher, D. Doktor, W. Lucht, J. Schaber, et al. 2004. Responses of spring phenology to climate change. *New Phytol.* **162**, 295–309.
- Bowyer, R. T., V. Van Ballenberghe, J. G. Kie, and J. A. K. Maier. 1999. Birth-site selection by alaskan moose: maternal strategies for coping with a risky environment. *J. Mammal.* **80**, 1070–1083.
- Brown, T. B., K. R. Hultine, H. Steltzer, E. G. Denny, M. W. Denslow, J. Granados, et al. 2016. Using phenocams to monitor our changing Earth: toward a global phenocam network. *Front. Ecol. Environ.* **14**, 84–93.
- Bubnicki, J. W., M. Churski, and D. P. J. Kuijper. 2016. trapper: an open source web-based application to manage camera trapping projects. *Methods Ecol. Evol.* **7**, 1209–1216.

- Burnham, K. P., and D. R. Anderson. 2004. Multimodel inference: understanding AIC and BIC in model selection. *Sociol. Methods Res.* **33**, 261–304.
- Burton, A. C., E. Neilson, D. Moreira, A. Ladle, R. Steenweg, J. T. Fisher, et al. 2015. Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. *J. Appl. Ecol.* **52**, 675–685.
- Denny, E. G., K. L. Gerst, A. J. Miller-Rushing, G. L. Tierney, T. M. Crimmins, C. A. F. Enquist, et al. 2014. Standardized phenology monitoring methods to track plant and animal activity for science and resource management applications. *Int. J. Biometeorol.* **58**, 591–601.
- Espmark, Y., and R. Langvatn. 1985. Development and habituation of cardiac and behavioral responses in young red deer calves (*Cervus elaphus*) exposed to alarm stimuli. *J. Mammal.* **66**, 702–711.
- Forrester, T., T. O'Brien, E. Fegraus, P. A. Jansen, J. Palmer, R. Kays, et al. 2016. An open standard for camera trap data. *Biodivers. Data J.* **4**, e10197.
- Hamel, S., S. T. Killengreen, J.-A. Henden, N. E. Eide, L. Roed-Eriksen, R. A. Ims, et al. 2013. Towards good practice guidance in using camera-traps in ecology: influence of sampling design on validity of ecological inferences. *Methods Ecol. Evol.* **4**, 105–113.
- Hertel, A. G., S. M. J. G. Steyaert, A. Zedrosser, A. Myrsterud, H. K. Lodberg-Holm, H. W. Gelink, et al. 2016. Bears and berries: species-specific selective foraging on a patchily distributed food resource in a human-altered landscape. *Behav. Ecol. Sociobiol.* **70**, 831–842.
- Hjeljord, O., N. Hövik, and H. B. Pedersen. 1990. Choice of feeding sites by moose during summer, the influence of forest structure and plant phenology. *Ecography* **13**, 281–292.
- Hoem, S. A., C. Melis, J. D. C. Linnell, and R. Andersen. 2007. Fighting behaviour in territorial male roe deer *Capreolus capreolus*: the effects of antler size and residence. *Eur. J. Wildl. Res.* **53**, 1–8.
- Hofmeester, T. R., J. M. Rowcliffe, and P. A. Jansen. 2017. A simple method for estimating the effective detection distance of camera traps. *Remote Sens. Ecol. Conserv.* **3**, 81–89.
- Hofmeester, T. R., J. P. G. M. Cromsigt, J. Odden, H. Andrés, J. Kindberg, and J. D. C. Linnell. 2019. Framing pictures: a conceptual framework to identify and correct for biases in detection probability of camera traps enabling multi-species comparison. *Ecol. Evol.* **9**, 2320–2336.
- Jachowski, D. S., T. Katzner, J. L. Rodrigue, and W. M. Ford. 2015. Monitoring landscape-level distribution and migration Phenology of Raptors using a volunteer camera-trap network. *Wildl. Soc. Bull.* **39**, 553–563.
- Liberg, O., A. Johansson, R. Andersen, and J. D. C. Linnell. 1998. Mating system, mating tactics and the function of male territoriality in roe deer. Pp. 221–256 in R. Andersen, P. Duncan and J. D. C. Linnell, eds. *The European roe deer: the biology of success*. Scandinavian University Press.
- Linnell, J. D. C., and R. Andersen. 1998. Timing and synchrony of birth in a hider species, the roe deer *Capreolus capreolus*. *J. Zool.* **244**, 497–504.
- Linnell, J. D. C., L. K. Wahlström, and J. M. Gaillard. 1998. From birth to independence: birth, growth, neonatal mortality, hiding behaviour and dispersal. Pp. 257–284 in R. Andersen, P. Duncan and J. D. C. Linnell, eds. *The European roe deer: the biology of success*. Scandinavian University Press, Oslo.
- Meek, P. D., G. Ballard, A. Claridge, R. Kays, K. Moseby, T. O'Brien, et al. 2014. Recommended guiding principles for reporting on camera trapping research. *Biodivers. Conserv.* **23**, 2321–2343.
- Melis, C., S. A. Hoem, J. D. C. Linnell, and R. Andersen. 2005. Age-specific reproductive behaviours in male roe deer *Capreolus capreolus*. *Acta Theriol.* **50**, 445–452.
- Mills, L. S., M. Zimova, J. Oyler, S. Running, J. T. Abatzoglou, and P. M. Lukacs. 2013. Camouflage mismatch in seasonal coat color due to decreased snow duration. *PNAS* **110**, 7360–7365.
- Mills, L. S., E. V. Bragina, A. V. Kumar, M. Zimova, D. J. R. Lafferty, J. Feltner, et al. 2018. Winter color polymorphisms identify global hot spots for evolutionary rescue from climate change. *Science* **359**, 1033–1036.
- Milner, J. M., C. Bonenfant, A. Myrsterud, J.-M. Gaillard, S. Csányi, and N. C. Stenseth. 2006. Temporal and spatial development of red deer harvesting in Europe: biological and cultural factors. *J. Appl. Ecol.* **43**, 721–734.
- Morisette, J. T., A. D. Richardson, A. K. Knapp, J. I. Fisher, E. A. Graham, J. Abatzoglou, et al. 2009. Tracking the rhythm of the seasons in the face of global change: phenological research in the 21st century. *Front. Ecol. Environ.* **7**, 253–260.
- Nijland, W., N. C. Coops, S. C. P. Coogan, C. W. Bater, M. A. Wulder, S. E. Nielsen, et al. 2013. Vegetation phenology can be captured with digital repeat photography and linked to variability of root nutrition in *Hedysarum alpinum*. *Appl. Veg. Sci.* **16**, 317–324.
- Pedersen, S., M. Odden, and H. C. Pedersen. 2017. Climate change induced molting mismatch? Mountain hare abundance reduced by duration of snow cover and predator abundance. *Ecosphere* **8**, e01722.
- Pfeffer, S. E., R. Spitzer, A. M. Allen, T. R. Hofmeester, G. Ericsson, F. Widemo, et al. 2018. Pictures or pellets? Comparing camera trapping and dung counts as methods for estimating population densities of ungulates. *Remote Sens. Ecol. Conserv.* **4**, 173–183.
- Plard, F., J.-M. Gaillard, T. Coulson, A. J. M. Hewison, D. Delorme, C. Warnant, et al. 2014. Mismatch between birth date and vegetation phenology slows the demography of roe deer. *PLoS Biol.* **12**, e1001828.
- Post, E., and N. C. Stenseth. 1999. Climatic variability, plant phenology, and northern ungulates. *Ecology* **80**, 1322–1339.

- Post, E., C. Pedersen, C. C. Wilmers, and M. C. Forchhammer. 2008. Warming, plant phenology and the spatial dimension of trophic mismatch for large herbivores. *Proc. Biol. Sci.* **275**, 2005–2013.
- Price, J. S., S. Allen, C. Fauchaux, T. Althnaian, and J. G. Mount. 2005. Deer antlers: a zoological curiosity or the key to understanding organ regeneration in mammals? *J. Anat.* **207**, 603–618.
- R Core Team. 2019. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Richardson, A. D., B. H. Braswell, D. Y. Hollinger, J. P. Jenkins, and S. V. Ollinger. 2009. Near-surface remote sensing of spatial and temporal variation in canopy phenology. *Ecol. Appl.* **19**, 1417–1428.
- Richardson, A. D., K. Hufkens, T. Milliman, D. M. Aubrecht, M. Chen, J. M. Gray, et al. 2018. Tracking vegetation phenology across diverse North American biomes using PhenoCam imagery. *Sci. Data* **5**, 180028.
- Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. *Nature* **421**, 57–60.
- Rovero, F., F. Zimmermann, D. Berzi, and P. Meek. 2013. “Which camera trap type and how many do I need?” A review of camera features and study designs for a range of wildlife research applications. *Hystrix* **24**, 148–156.
- RStudio Team. 2016. *RStudio: integrated development for R*. RStudio, Inc., Boston, MA. <http://www.rstudio.com/>
- Sirén, A. P. K., M. Somos-Valenzuela, C. Callahan, J. R. Kilborn, T. Duclos, C. Tragert, et al. 2018. Looking beyond wildlife: using remote cameras to evaluate accuracy of gridded snow data. *Remote Sens. Ecol. Conserv.* **4**, 375–386.
- Sonnentag, O., K. Hufkens, C. Teshera-Sterne, A. M. Young, M. Friedl, B. H. Braswell, et al. 2012. Digital repeat photography for phenological research in forest ecosystems. *Agric. For. Meteorol.* **152**, 159–177.
- Steenweg, R., M. Hebblewhite, R. Kays, J. Ahumada, J. T. Fisher, C. Burton, et al. 2017. Scaling-up camera traps: monitoring the planet’s biodiversity with networks of remote sensors. *Front. Ecol. Environ.* **15**, 26–34.
- Visser, M. E., and C. Both. 2005. Shifts in phenology due to global climate change: the need for a yardstick. *Proc. Roy. Soc. Lond. B: Biol. Sci.* **272**, 2561–2569.
- Wam, H. K., A. M. Felton, C. Stolter, L. Nybakken, and O. Hjeljord. 2017. Moose selecting for specific nutritional composition of birch places limits on food acceptability. *Ecol. Evol.* **8**, 1117–1130.
- Welbourne, D. J., A. W. Claridge, D. J. Paull, and A. Lambert. 2016. How do passive infrared triggered camera traps operate and why does it matter? Breaking down common misconceptions. *Remote Sens. Ecol. Conserv.* **2**, 77–83.
- Zeileis, A., F. Leisch, K. Hornik, and C. Kleiber. 2002. strucchange: an R package for testing for structural change in linear regression models. *J. Stat. Softw.* **1**, 1–38.
- Zeileis, A., C. Kleiber, W. Krämer, and K. Hornik. 2003. Testing and dating of structural changes in practice. *Comput. Stat. Data Anal.* **44**, 109–123.

Supporting Information

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

Figure S1. Map of the study area. Each black point represents a camera trap location where a single camera was deployed for 6–10 weeks. Red points represent cameras that were not taken into account in the analyses for reasons outlined in the main text. Black squares show the locations of the two weather stations from which data were used.

Figure S2. Camera trap pictures of mountain hares (*Lepus timidus*) in different stages of moulting, used as template for classification.

Data S1. Detailed analyses of camera-derived temperature data compared to local weather station.

Data S2. Daily averages of midday temperature and snow cover as used in the analyses.

Data S3. Weekly averages of plant and mountain hare (*Lepus timidus*) phenology as used in the analyses.