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METHODS, TOOLS, AND TECHNOLOGIES

Using remote cameras to measure seasonal molts

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Abstract. Obtaining accurate data on seasonal timing of lifecycle events in the wild is critical for many aspects of ecological research. However, characterizing such phenological processes is difficult, expensive, and time consuming. Remote camera traps are increasingly used in ecology, yet their potential to study key phenological traits in animal populations has been largely unexplored. Here, we examine the potential of remote camera traps to measure the progression of seasonal molts in mammals. We evaluated the accuracy of trained observers to classify the stage of molt from camera-trap images and identified factors that increase the accuracy of this method in a common, color molting mammal, the snowshoe hare (*Lepus americanus*). Our results showed that images taken by remote camera traps can be used to classify the stage of color molt with relatively high accuracy (i.e., 84%). Observers achieved the highest accuracy when using a classification protocol with fewer molt categories, and from images acquired during the day. We also found that hare body position in the image, and whether the hare was moving or still had small influences on observer classification accuracy. Camera model had negligible effect on accuracy. Overall, our results suggest that camera traps can be used to classify molt progression to measure molt phenology in the wild. Because many camera-trap studies are ongoing around the world, images of species that undergo distinguishable seasonal molts could be pooled across studies to characterize molt phenology on local and global scales. In much the same way that remote cameras have revolutionized the study of distribution, abundance, and behavior of some animal populations, so too can remote camera images transform our understanding of key phenological processes across space, time, and taxa.

Key words: color molting mammals; molt classification; phenology; remote camera traps; seasonal molt; snowshoe hare.

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Introduction

Characterization of phenology, the seasonal timing of lifecycle events, is fundamental for understanding animal ecology and evolution, particularly as global anthropogenic change alters phenology in many natural systems (Parmesan and Yohe 2003, Cohen et al. 2018). For example, climate change has shifted the phenology of reproduction in amphibians (While and Uller 2014), migration in birds (Charmantier and Gienapp 2014, Socolar et al. 2017), and hibernation in mammals (Adamík and Král 2008, Ozgul et al. 2010). Mismatches arising from disparate shifts between climate and phenological traits can negatively impact fitness, especially when the shifts vary across trophic levels (Both et al. 2006, Post and Forchhammer 2008, Doiron et al. 2015, Zimova et al. 2016, Visser and Gienapp 2019). However, phenology monitoring is difficult and expensive, especially given the frequency of sampling required and the spatial and temporal scales necessary for a rigorous characterization of prolonged, complex life events.

Remote camera traps allow relatively inexpensive monitoring across large geographical scales, and their use in ecological research has expanded rapidly in recent decades. Camera traps are now commonly used to characterize wildlife distribution, abundance, and behavior (for reviews, see O'Connell et al. 2011, Burton et al. 2015, Caravaggi et al. 2017), with increasing potential to do so on a global scale (Steenweg et al. 2017). However, published studies using remote cameras to quantify phenology remain relatively rare (but see Tape and Gustine 2014, Jachowski et al. 2015, Hofmeester et al. 2019, Zimova et al. 2020) or used specialized, automated time-lapse photography (Black et al. 2018, Hinke et al. 2018). Given the hundreds of ongoing camera studies globally, especially for mammals, the untapped use of camera images represents an exciting opportunity to study phenological processes and their potential mistiming with environmental conditions under climate change across spatial, temporal, and taxonomic scales.

Seasonal molting in birds and mammals is a key phenological trait, recently garnering increased attention in the context of climate change (Mills et al. 2018, Zimova et al. 2018). Most bird and mammal species occupying temperate and polar ecosystems partially or completely replace thinner summer pelage or plumage with a warmer winter coat (Beltran et al. 2018). Additionally, in 21 species (18 mammals, 3 birds) the new winter coat or plumage is white instead of brown to increase camouflage against snow-covered landscapes in parts of their range (e.g., snowshoe hares *Lepus americanus*, short-tailed weasels *Mustela erminea*, willow ptarmigan *Lagopus lagopus*; Zimova et al. 2018). But the shifting climatic conditions may create phenological mismatches among the molts and temporal variation in temperature/snow cover presence. In color molting species, the shortening duration of snow cover results in camouflage mismatch between white winter coats and dark snowless ground (Mills et al. 2013), leading to decreased survival (Zimova et al. 2016, Atmeh et al. 2018, Wilson et al. 2018). Additionally, potential phenological mismatch between other photoperiod-driven seasonal molts and warming temperatures may increase risk of heat stress (Sarmento et al. 2019) as winter coat is much warmer than its summer counterpart (Zimova et al. 2018). Measuring molt phenology across time and space is therefore important for understanding molting species vulnerability to associated phenological mismatches under climate change (Zimova et al. 2020)

Although seasonal molts are of high adaptive significance (Beltran et al. 2018, Zimova et al. 2018) and their mistiming with the environmental conditions can have negative fitness consequences (e.g., Zimova et al. 2016, Wilson et al. 2018), molt phenology within and among species is poorly understood. The primary barriers include difficulties associated with phenology quantification and monitoring, exacerbated by the prolonged duration of molts (i.e., 1–2 months each spring and fall; Zimova et al. 2018) and the remoteness and ruggedness of areas typically inhabited by these seasonally molting species. To date, information on molt phenology in wild animals has been mainly acquired via radiotelemetry (Mills et al. 2013, Zimova et al. 2014, 2016, Wilson et al. 2018), periodic field surveys (Watson 1963, Tomotani et al. 2018, Beltran et al. 2019), and retrospective examinations of specimens in museum collections (Salomonsen 1939, Hall 1951, Kiat et al. 2019). Although these methods have proven effective, they are often invasive, expensive, and/or time consuming. Noninvasive methods, such as remote camera trapping, that do not require physically seeing the animal are necessary to generate sufficient data to quantify molt phenology in elusive species across time and space. This has been recently accomplished in the wild (Hofmeester et al. 2019, Zimova et al. 2020).

Here, we describe and validate the capacity of remote, motion-triggered camera traps to yield accurate estimates of molt progression. We assessed the accuracy of human observers in classification of coat color molt categories from camera-trap images in snowshoe hares and determined what factors affect the accuracy of the molt phenology estimates among observers.

Additionally, we provide protocols for the classification of color molt progression in snowshoe hares and give broad recommendations for quantification of molt phenology in the wild.

Methods

Animals and experimental pens

We conducted this study using eight captive snowshoe hares (five females, three males) housed at an outdoor facility at the University of Montana (UM) in Missoula, Montana. Animals were housed in all-female and all-male groups in outdoor aviaries (approximately 8 × 15 m), exposed to natural environmental conditions. Water and rabbit food (Sherwood Pet Health, Logan, Utah, USA) were available ad libitum during both camera-trapping sessions and during non-experimental conditions. Five individuals were originally captured in the wild in the Seeley-Swan Valley, Montana or Cascade Mountains, Washington, and three individuals were their captive-born offspring. All individuals underwent the typical coat color molt to white winter fur. The UM Institutional Animal Care and Use Committee approved all husbandry, handling, and experimental procedures (protocol 46-17).

For this study, individual hares were transferred to 2.4 × 2.4 m experimental outdoor pens. The pens received natural light, with floors covered by a random arrangement of brown and white 0.3 × 0.3 m colored foam mats to resemble patches of bare ground and snow. Two models of motion-triggered cameras with infrared flash were mounted within the pens: the more expensive Reconyx PC900 HyperFire Professional camera (~USD $550/camera, Holmen, Wisconsin, USA), and the more economical Browning Strike Force (~USD $150/camera). Cameras were mounted next to each other, approximately 20 cm above the ground. Both cameras were set to the same settings (i.e., 5-megapixel resolution, 3 images per trigger, and 10-s intervals).

Camera-trapping sessions

We developed two protocols to classify the stage of snowshoe hare molt from camera-trap images using either three or five predefined categories (Appendix S2). Both classification protocols were based on the percentage of hare's body that is white (Fig. 1). The five-category protocol included 0, 25, 50, 75, and 100% white categories and was based on a previously developed protocol used to classify color with field observers (Mills et al. 2013; Fig. 1). The simplified three-category protocol included 0, 50, and 100% white categories and was recently implemented to quantify molt phenology from remote camera-trap images in snowshoe hares (Zimova et al. 2020).

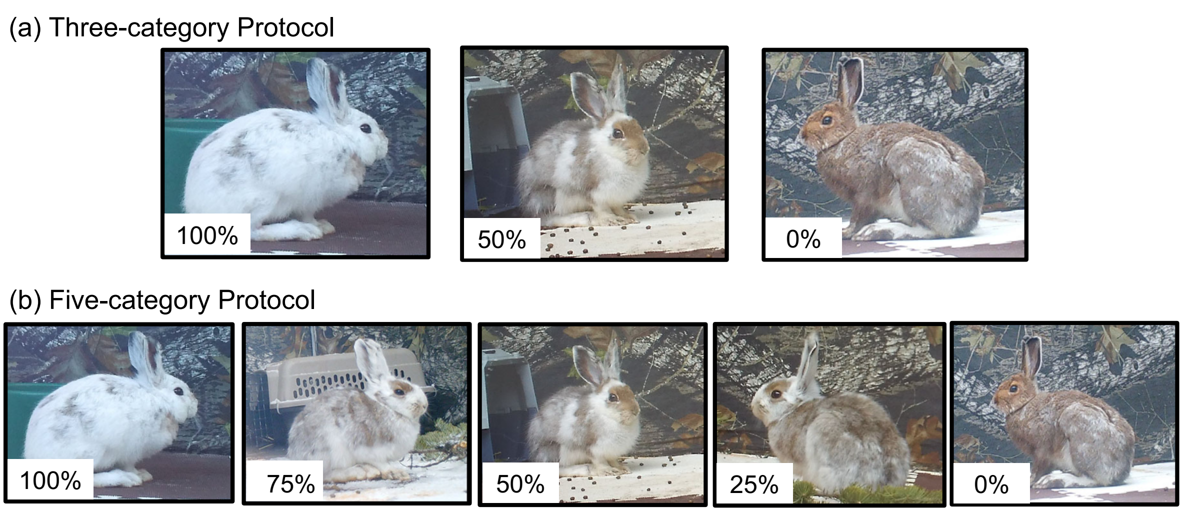

Fig. 1. Snowshoe hare coat color during molt according to the (a) three- and (b) five-category protocols. Full protocols and molt stage descriptions available in Appendix S2.

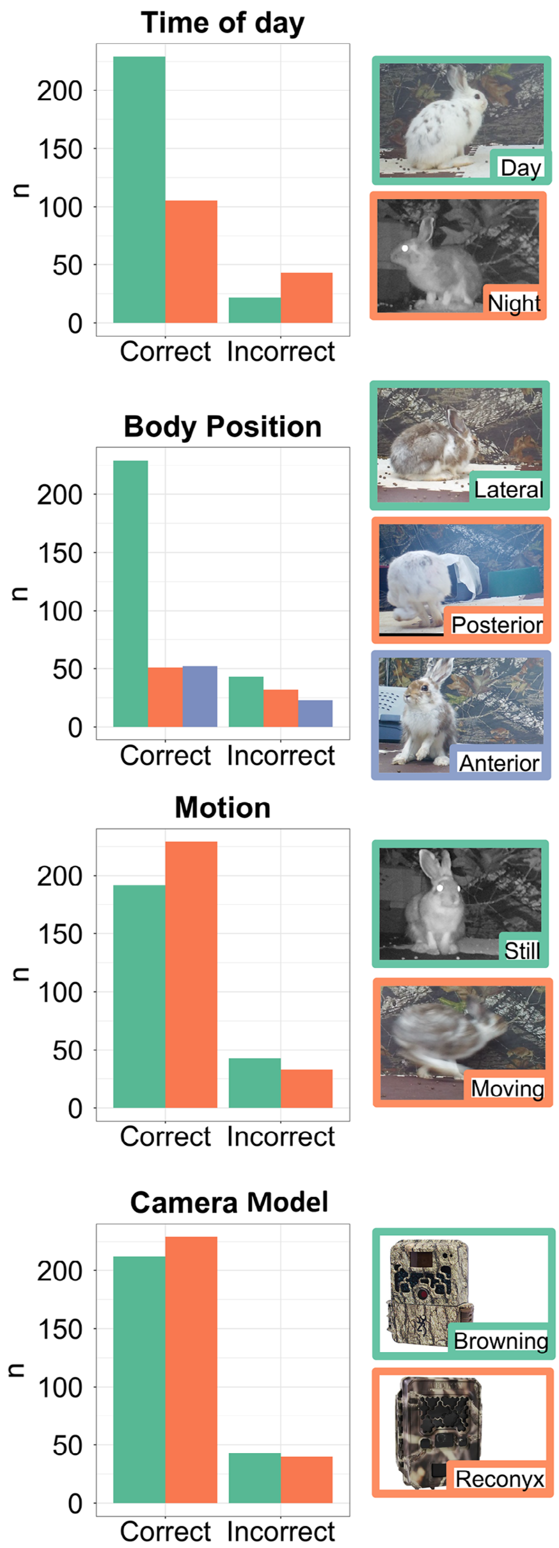

Fig. 2. Number of correctly and incorrectly classified images (n) using the three-category protocol

(Fig. 2. *Continued*)

colored by time of day, hare body position, hare motion, and camera model. All but camera model were significant predictors of accuracy to classify molt stages from camera-trap images using the three-category protocol.

One hare with a known stage of coat color molt was placed in the experimental pen and photographed for approximately 48 h (camera-trapping session). The hare's true color was based on a consensus of two observers (LB and MZ) by direct visual observation prior to each camera-trapping session, using both classification protocols (Fig. 1). We carried out ten camera-trapping sessions total, so that we photographed two different individuals per each of the five molt categories.

Image classification

One observer (LB) selected a set of 240 images that showed the entire hare's body. These images consisted of all ten sessions, each with 24 total combinations of variables of interest: time of day (day, night), hare motion (still, moving), hare body position relative to the camera (lateral, anterior, posterior), and camera model (Reconyx, Browning; Fig. 2). All images were randomly named and sorted, with the dates and manufacturer's logos removed to minimize observer expectancy bias.

The molt classification protocol (Appendix S2) and the full collection of randomly sorted images were supplied to 18 participants (faculty or students) with backgrounds in ecology-related disciplines from University of Montana or Northern Michigan University. Participants classified coat color molt stage in each image using both protocols and gave each score a subjective measure of confidence in their classification (low, medium, or high).

Statistical analysis

We used Program R (Version 3.5.3) and R Studio (Version 1.1.463) to conduct all statistical analyses (R Development Core Team 2019). We evaluated the accuracy of estimating hare color molt progression based on camera-trap images as the proportion of correctly classified images across all participants. An image was considered as correctly scored when the observer's classification of hare's molt stage equaled the hare's true molt stage. The accuracy was calculated separately for molt stage estimates based on each classification protocol. Finally, we calculated accuracy using two subsets of the data: one excluding low confidence estimates and one including only high confidence estimates.

Next, we tested the effects of different factors on the accuracy of coat color molt stage classification. We fit linear mixed models with a binomial response (correct or incorrect classification) using package lme4 (Bates et al. 2015). Models included time of day, motion, body position, and camera model as fixed effects; and participant, hare ID, and photo-session as random effects. In addition, we included two interactions terms as fixed effects: (1) interaction between camera model and time of day, and (2) between camera model and motion. We fit separate models for each set of molt stage estimates (the three- vs. five-category protocols). We tested for correlations between all categorical covariates (i.e., time of day, motion, body position, and camera model) using Pearson's chi-squared test and found no correlations at the $P < 0.05$ level.

Results

Observer accuracy in estimating molt stage from remote camera images varied by classification protocol, with all participants achieving higher accuracy using the protocol with fewer categories (Table 1). The accuracy was similar across the 18 participants, except for one participant with exceptionally low number of correctly classified images, especially when using the three-category protocol (48 out of 240 images). Across the 18 participants, image classification accuracy was 84% (SD = 10%) with the three-category protocol, vs. 62% (SD = 12%) with five categories (Table 1). The mean percentage of correctly classified images was higher when using estimates ranked with higher confidence (e.g., 89%, SD = 11% for the three-category protocol and 75%, SD = 17% for the five-category protocol for high confidence scores; Table 1; Appendix S1).

When using the three-category protocol, all factors but camera model and the two interactions significantly influenced accuracy of estimating molt stage (after accounting for the random effects of participant, individual hare and session; Table 2a, Fig. 2). Images taken during the day were 5.7 times more likely to be classified correctly compared to images taken at night (Table 2a, Fig. 2). Body position was the second most important predictor, with images of hares

Table 1. Accuracy as mean and standard deviation of percentage of correctly classified images using three or five molt stage categories and using data with different score confidence levels.

Confidence	3 categories	5 categories	No. of observations
All levels (%)	83.5 (9.6)	62.2 (12.1)	4320
High, medium (%)	85.7 (9.2)	65.0 (12.9)	3788
High (%)	89.4 (11.1)	74.8 (16.6)	2131

Notes: Standard deviation is given in parentheses. All levels include high, medium, and low confidence. Number of observations indicates number of images in each data set.

Table 2. Effect size of factors affecting accuracy of estimating molt stage from camera-trap images, expressed as odds ratio and 95% confidence intervals.

Factor	Odds ratio	95% CI	
		Lower	Upper
(a) 3-category protocol			
Time Night*	0.174	0.132	0.229
Motion Still*	1.396	1.091	1.786
Position Lateral*	1.957	1.520	2.519
Position Posterior*	1.720	1.262	2.345
Camera Reconyx	1.127	0.773	1.642
Camera Reconyx: Time Night	1.165	0.781	1.739
Camera Reconyx: Motion Still	0.998	0.697	1.429
(b) 5-category protocol			
Time Night*	0.199	0.160	0.247
Motion Still	1.171	0.946	1.449
Position Lateral*	2.120	1.675	2.683
Position Posterior*	1.702	1.288	2.250
Camera Reconyx	0.782	0.599	1.021
Camera Reconyx: Time Night*	1.768	1.312	2.383
Camera Reconyx: Motion Still	0.911	0.676	1.227

Notes: Examined factors (time of time of day, hare motion, hare position, camera model) are listed for both the (a) three- and (b) five-category protocols. Significant effects were evaluated at the $\alpha = 0.05$ and are indicated by asterisks.

taken from the side (lateral) and from the posterior approximately twice as likely to be correctly classified compared to anterior images of hares (Table 2a, Fig. 2). Images of still hares were 1.4 times more likely to be classified correctly compared to images taken of moving hares (Table 2a, Fig. 2). The results were similar using five categories, except hare motion was not a significant predictor of accuracy, and the interaction between camera model and time of day was significant (Table 2b). Specifically, night images taken by the Rexonyx camera were slightly more often scored correctly compared to those by Browning (54% vs. 48% correctly scored), but daytime Reconyx images were slightly less often scored correctly compared to those by Browning —yet this difference was even smaller (72% vs. 75% correctly scored; Appendix S1: Fig. S2).

Discussion

We described and validated a new method to generate reliable data for quantifying molt phenology using remote camera traps. Our results showed that camera-trap images can be used to classify the progression of molts in a color molting species with relatively high accuracy (i.e., 84%). Additionally, we found ways to increase accuracy of molt stage estimates by using fewer molt categories for classification and by using images acquired during the day. Below, we discuss the multiple factors that affect the accuracy of the molt stage estimation from camera traps and provide recommendations for the method's application in the field.

Overall, participants achieved higher accuracy in estimating coat color molt stage when using fewer molt categories. Specifically, using three vs. five molt stage categories improved accuracy by approximately 20% (Table 1). Further, using scores with higher confidence increased accuracy (Table 1). For example, using high confidence scores only vs. all scores increased overall accuracy by 5% for the three-category and 13% for the five-category protocol. However, excluding images with lower confidence quickly decreased sample size (Table 1). Therefore, if statistical power is of concern, researchers should use all images and accept a relatively low loss in accuracy to increase power. However, in case of large, multi-study data sets, the most effective approach is to include only high confidence estimates.

Of the factors we considered (Table 2, Fig. 2), time of the day had the highest influence on accuracy of molt stage estimates, with night images having lower accuracy (Table 2 for night, 94% for daytime, Fig. 2). However, many species are crepuscular and nocturnal, and night-time images may represent a large portion of the data set. Therefore, unless sample sizes of daytime images are high, we recommend using both night- and daytime images in molt phenology quantification. Our camera models used infrared technology, which results in black and white images at night. Discerning molt categories from monochrome images is more difficult and could potentially be eliminated by using cameras with white flash, although white flash cameras may cause a startle response in some nocturnal species (Wegge et al. 2004, Meek et al. 2014). Furthermore, we found that night images produced by the more expensive Reconyx cameras were classified correctly more often than the night images produced by the Browning cameras (54% vs. 48% at the five-category scale only; Table 2; Appendix S1). Such a 6% difference is negligible, however, implying that researchers do not need to employ more expensive cameras to accurately estimate molt stages and images—and resulting data—may be combined across studies using different camera models.

Hare's body position in the image had some effect on accuracy (Table 2). Based on our results, we recommend using images depicting the animals' lateral or posterior view, and when possible combining multiple images from the same encounter to estimate molt stage. To maximize the number of images from different angles, researchers can set cameras to take multiple images per trigger or include a second camera at each station. Next, images including still animals resulted in higher accuracy than when animals were moving, but the overall increase in accuracy was relatively low (4%, Fig. 2).

Our results with snowshoe hares should be broadly applicable, both to the other 20 color molting species and to the many other species that undergo distinguishable seasonal molts. Seasonally molting species that undergo the brown-to-white color molts (such as hare spp. *Lepus*, Arctic foxes *Alopex lagopus*, and ptarmigan spp.

Lagopus) are routinely captured on cameras (e.g., Tape and Gustine 2014, Davis et al. 2019), and their molts show similar progression across the body (for detailed molt progression descriptions see Zimova et al. 2018). The potential of camera-trap images to quantify molt phenology (e.g., initiation date, molt duration, etc.) using different statistical frameworks has been recently demonstrated using molt stage estimates based on the three-category color scale in snowshoe hares (Zimova et al. 2020) and a different four-category scale in mountain hares (*Lepus timidus*; Hofmeester et al. 2019). Beyond seasonal color-changing species, molt progression can be followed visually, without handling, in other mammals and birds (e.g., mountain goats *Oreamnos americanus*, Déry et al. 2019; pygoscelid penguins, Black et al. 2018) and may also be of interest. In short, motion-triggered cameras could transform study of molt phenology for both the 21 color molting species and for other molting mammals and birds.

We demonstrate that camera-trap images can be used to accurately estimate molt progression stages to derive molt phenology. As a noninvasive, less field-time intensive alternative to direct observation by field workers, camera traps allow real-time, long-term monitoring across large geographical areas (e.g., Steenweg et al. 2016, Rich et al. 2017). Furthermore, many ongoing camera studies already capture, but do not use, images from seasonally molting species (photographic bycatch). Thus, we encourage combining images from multiple independent studies or sharing data in global biodiversity archives (e.g., Global Biodiversity Information Facility [www.gbif.org], eMammal [McShea et al. 2016, emammal.org]) to effectively monitor molt phenology across spatial, temporal, and taxonomic scales. Remote camera traps have the potential to radically improve our understanding of molt phenology, its variation in space and time, and its role in illuminating ecological consequences of climate change.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3084/full