# Survival of a polymorphic species in seasonally snow-covered forests

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## Abstract

Color polymorphism is an adaptive strategy in which a species exhibits multiple color phenotypes in a population. Often times, phenotypes are variably suited to different environmental conditions which may buffer the population against variable conditions. Modern climate change is creating novel selective pressures for many species, especially in winter habitats. Few studies have quantified the benefits of polymorphism for allowing species to cope with climate-induced environmental change. We investigated how color polymorphism mediates selective pressures in ruffed grouse Bonasa umbellus, a widespread and winter-adapted bird species of North American forests. Ruffed grouse display phenotypic variation in plumage color, ranging from red to gray. Over five winter seasons (2015-2022), we monitored weather conditions, habitat use, and weekly survival for 94 ruffed grouse to test whether individuals had lower survival when grouse were phenotypically mismatched with snow cover (e.g., a gray bird on a snowless landscape or a red bird in snow). Grouse phenotypically mismatched with snow cover had lower survival, but only when winter survival rates were lowest. During winters of lower overall survival, red grouse exhibited higher survival during snow-free periods, whereas gray grouse had higher survival when snow was present. We also found that open habitat negatively impacted survival, regardless of color. While the effect of phenotypic mismatch was variable among years, it was a stronger predictor of winter survival than land cover features, suggesting that snow is an important habitat feature mediating overwinter survival. Our work offers an advancement in understanding how environmental variability affects geographic variation in and maintenance of multiple color phenotypes in seasonally-snow covered environments. Our finding that interactions between color morph and snow cover are important for conferring winter survival provides further evidence that color polymorphism may serve as a buffer against rapidly changing conditions and a pathway for persistence of polymorphic species.

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### Keywords

Bonasa umbellus, ruffed grouse, color polymorphism, phenotypic mismatch, winter ecology, Wisconsin

## Introduction

Animals exhibit great variation in coloration both within and among species. Which colors persist and how these colors are arranged reflects an optimization of competing adaptive functions including sexual selection, thermoregulation, and camouflage (Walsberg et al. 1978, Endler 1981, Andersson 1994, Stuart-Fox et al. 2017). Often, coloration covaries with the environment when the adaptiveness of coloration depends on how color and environment interact to influence individual fitness (Cott 1940, Cuthill et al. 2017, Barrett et al. 2019). Over evolutionary time, spatial and temporal changes in environmental conditions can produce multiple color phenotypes in a population, or color polymorphisms (Bell 2010, McLean and Stuart-Fox 2014). Stable color polymorphism is defined as the persistence of intraspecific variation in coloration between sympatric individuals of the same age group that is genetically inherited and the expression of which is not sensitive to changes in body condition, diet, or environment (Huxley 1955, Roulin 2004). Color polymorphism occurs across a myriad of vertebrates (e.g., mammals, reptiles, and birds) and is considered essential for enabling species to respond to environmental gradients associated with habitat type (Hoekstra et al. 2004), vegetation cover (Baling et al. 2020), weather (Galeotti et al. 2009), and pollution (Kettlewell 1955, Bishop 1972).

In high-latitude ecosystems, winter is characterized by freezing temperatures and snow cover, a seasonal and dynamic environmental feature that is important habitat for winter-adapted species. Snow has implications for enhancing crypsis for polymorphic species and species that exhibit seasonal coat color change. Twentyone species of birds and mammals exhibit seasonal molt changes from brown to white during the winter allowing for greater camouflage on the snowy landscape (Grange 1932, Cott 1940, Mills et al. 2018). This phenotypic trait is an adaptation to seasonal snow cover duration with potentially strong fitness consequences. In some cases, when the rate of seasonal molt change no longer matches the rate of snow cover change, a phenological mismatch occurs. For example, seasonally molting rock ptarmigan Lagopus mutus and snowshoe haves Lepus americanus that are phenotypically mismatched with a snowless environment (due to the loss of snow cover) exhibit lower survival during the winter months (Wilson et al. 2019, Melin et al. 2020). This phenotypic mismatch between white body coloration and snowless habitat has potentially strong implications for population persistence, especially along southern range boundaries where climate change-induced snow loss is shortening snow season length and increasing periods of mismatch (Montgomerie et al. 2001, Mills et al. 2013, Wilson et al. 2019). Similarly, for species that do not undergo seasonal molts, environmental gradients (e.g., precipitation, land cover), and periods of rapid environmental change are thought to be maintaining forces for color polymorphism (Galeotti and Sacchi 2003, Roulin 2004). For example, variability in annual snowfall and temperature is likely an important selective force on plumage polymorphism in the tawny owl *Strix aluco*, where survival of the gray morph is higher than that of brown morphs during snowier winters (Galeotti and Cesaris 1996, Karell et al. 2011).

The ruffed grouse *Bonasa umbellus* is a winter-adapted galliform that occupies young forest across North America (Rusch et al. 2020) and is polymorphic with two predominant color morphs of red or gray, although intermediates frequently occur (Bump et al. 1947, Rusch et al. 2020). The genetic basis of color morphs in ruffed grouse has not been described, though it is thought to be a melanin-based genetic color polymorphism, which is the basis for red/brown polymorphisms across most bird species (Roulin 2004, Mundy 2005). Throughout their range, the survival rates of ruffed grouse vary seasonally and geographically (Devers et al. 2007, Zimmerman et al. 2007, Wilson et al. 2022), but little research has investigated possible

demographic differences between grouse color morphs. Winter is an important demographic constraint for grouse populations in the upper midwestern United States where mortality, mostly due to predation, is highest during the winter months (Small et al. 1991, Gutiérrez et al. 2003, Pomara and Zuckerberg 2017). Ruffed grouse burrow in deep snow to evade predators and cold ambient temperatures (Shipley et al. 2019, 2020, 2022), and overwinter mortality is associated with shallow snow cover (Shipley et al. 2020), but little is known about how phenotypic matching with snow might impose differential survival for red and gray morphs.

Geographic clines in polymorphic traits can provide important insights into the selective pressures that drive the persistence of polymorphism as an adaptive strategy (Levins and MacArthur 1966, Takahashi 2015). For ruffed grouse, it has been suggested that there is geographic variation in color morph ratios across their range that covaries with latitude and winter conditions, although this has not been formally described (Bump et al. 1947, Rusch et al. 2020). Past authors have speculated that red and gray morphs are differently sensitive to snow cover; suggesting that there may be higher proportions of gray individuals found at more northerly latitudes whereas red individuals are more associated with southerly and coastal areas with lower snowfall (Gullion 1984, Rusch et al. 2020). There is some evidence to suggest daily ruffed grouse survival differs by season between morphs, but the relationship between winter survival by morphs and snow cover has not been tested in northern, seasonally dynamic ecosystems (but see: Gutiérrez et al. 2003).

Ruffed grouse occupy a range of different forest types and ages but are closely associated with young successional forests (Zimmerman et al. 2009, Tirpak et al. 2010). The presence of young forest and dense cover may offset the costs of phenotypic mismatches during winter. For snowshoe hares, occupying patches of dense young aspen negated the mortality associated with phenotypic mismatch (i.e., white snowshoe hares on bare ground) (Wilson et al. 2019). In addition to this potential buffering of phenotypic mismatch by forest cover, snow presence and duration of seasonal snow cover varies across different forest cover types (Petty et al. 2015). Forest canopy cover accounts for 57% and 72% of the variance in snow accumulation and ablation, respectively (Varhola et al. 2010), and forest understory density can alter ambient temperature and solar radiation that reaches the ground, which in turn, alters snow cover depth and persistence (Lundquist et al. 2013, Petty et al. 2015).

Our goal was to examine phenotype-by-environment interactions between color morph and snow cover and its role in mediating overwinter survival in ruffed grouse. We used a five-year dataset of overwinter survivorship for a population of ruffed grouse in central Wisconsin to investigate potential effects of snow cover and habitat on individual survival of ruffed grouse. We hypothesized that snow cover and habitat characteristics would differently affect red and gray morph winter survival. Under this hypothesis, we predicted that individuals who were phenotypically mismatched to the surrounding winter landscape would have lower survival. In other words, gray morphs would experience lower survival during periods with less or patchier snow cover (Fig. 1). Conversely, red morphs would experience lower survival during periods of more persistent snow cover (Fig. 1). We further predicted that the cost of phenotypic mismatch would be lower for individuals inhabiting areas of dense cover such as young aspen forest (Wilson et al. 2019).



**Figure 1.** Predicted relationship between ruffed grouse *Bonasa umbellus* overwinter survival and phenotypic mismatch caused by mismatch between plumage coloration (color morph) and snow presence or absence. (a) We predicted that gray morph birds would have lower survival during periods with less or patchier snow cover and red morph birds would have lower survival during periods of more persistent snow cover. (b) Ruffed grouse exhibit variation in plumage coloration with two predominant color morphs of red or gray, although intermediates frequently occur and differences are most pronounced in tail fan coloration. Photographs by Joanne King (left) and Simon Boivin (right).

# Material and methods

# Study system

Research was conducted at Sandhill State Wildlife Area (44.31°N, -90.13°W; hereafter, Sandhill), a 36 km<sup>2</sup> wildlife area located within the biological tension zone of central Wisconsin in the midwestern region of the United States (Fig. 2). Sandhill is enclosed by a 2.75 m-tall fence and managed by the Wisconsin Department of Natural Resources to maintain habitat for several species, including ruffed grouse. Sandhill is a complex mosaic of forest types and age classes separated by a network of managed flowages and marshes; the dominant forest types are aspen *Populus tremuloides* and *P. grandidentata* and oak and scrub oak *Quercus* sp. forests (Shipley et al. 2019). Public vehicle access to Sandhill is restricted throughout winter, but there is a limited fall hunting season for ruffed grouse in the southern half of Sandhill.

Grouse are subject to predation from a diverse suite of predators across their range, many of which are found at Sandhill including great horned owl *Bubo virginianus*, barred owl *Strix varia*, sharp-shinned hawk *Accipitier striatus*, Cooper's hawk*Accipiter cooperii*, northern harrier *Circus hudsonius*, bobcat *Lynx rufus*, and coyote *Canis latrans* (Rusch et al. 2020). Grouse populations in the midwestern United States are most vulnerable to predation by hawk and owl species, all of which have high visual acuity and ability to distinguish colors in the visible light spectrum (Small et al. 1991, Höglund et al. 2019). While some species of predators hunt more nocturnally, all also exhibit crepuscular or diurnal hunting activity which coincide with times that grouse are most active (Hewitt and Kirkpatrick 1997, Passarotto et al. 2018).



Figure 2. Map of ruffed grouse winter use areas (2015-2022) within our study site at Sandhill State Wildlife Area in central Wisconsin, United States. Land cover data shown is from winter of 2021, adapted from Wilson et al. 2019.

Grouse trapping and winter tracking

From September through November, we trapped ruffed grouse using mirror traps and walk-in funnel traps attached to a wire drift fence (Gullion 1965). We covered traps with vegetation to provide camouflage from predators and checked traps twice daily. We fitted grouse with VHF radio-collars (12 g, necklace-style, 4h or 6h mortality signal, Advanced Telemetry Systems Inc, Isanti MN) and uniquely numbered aluminum leg band (National Tag and Band Company, Newport KY). We measured body mass, tarsus length, bill length and assigned color morph variant, red or gray, by examining central tail feather coloration. We aged (juvenile or after-hatch-year adult) and sexed each individual according to standard criteria (Hale et al. 1954). We immediately released grouse after processing. We trapped grouse in the fall over 5 seasons: 2015 - 17 (Shipley et al. 2020) and 2020 - 2021.

Through winter (December through March), we obtained radiolocations of collared individuals 1-2 times a week between the hours of 0900 and 1700 using a handheld receiver and a three-element Yagi antenna (Advanced Telemetry Systems Inc, Isanti MN). When a mortality signal was detected, we determined cause of death by assessing for evidence of predation within 1-2 days of the signal (Bumann and Stauffer 2002).

## Winter weather and land cover

From relocations and original trap locations, we constructed 75% minimum convex polygons (MCPs) using the R package 'adehabitatHR' to represent individuals' core area of use throughout the winter for birds with greater than or equal to 10 locations (Fig. 2, n = 64, R Core Team 2021, Calenge 2006). For individuals with less than 10 locations, we created buffered centroids equal to the mean MCP area (12.02 ha, n = 30). We explored 50%, 75%, and 95% MCP and kernel density estimates for calculating winter ranges. We chose to use MCPs at the 75% level to represent the core area of an individual's winter use areas as peripheral areas in an animal's home range are difficult to identify with telemetry data and may have reduced biological significance (Powell 2000, Whitaker et al. 2007). Additionally, we found no evidence for a linear relationship between the estimated 75% MCP area and either number of radiolocations or duration of monitoring ( $F_{1,69}$ = 3.30, p = 0.08).

To characterize environmental conditions encountered by individuals throughout winter, we extracted daily snow data and minimum daily temperature data at 1-km resolution from Snow Data Assimilation System (SNODAS, National Operational Hydrologic Remote Sensing Center 2004) and Daymet, accessed through the 'daymetr' package in R (Hufkens et al. 2018, Thornton et al 2020, 2021). We used snow depth from SNODAS to determine snow presence or absence. Values were spatially averaged across individual winter use areas using the 'exact extractr' package (Baston 2022).

To capture important landscape metrics within an individual winter use area, we calculated class-level landscape metrics on reclassified rasterized data from the Wisconsin Forest Inventory Map (WisFIRS; WDNR). The reclassified data layers were adapted from methods reported in Wilson et al. 2019 and contained 5 cover types: "Dense Cover" (< 20 yr aspen or alder stands), "Mature Forest" (> 20 yr stands), "Open" (emergent vegetation, lowland brush/willow, and lowland grass), "Clear Cut" (< 4 yr since harvest), and "Other" (all other cover classes; mostly open water and marsh). We classified areas as Clear Cut for three years following harvest as recruitment of aspen suckers into the sapling stage begins roughly four years after harvest (Bose et al. 2014). We classified small areas not covered by WisFIRS (e.g., private lands) using leaf-on and leaf-off NAIP imagery and field data (OCM Partners 2022). We rasterized the land cover data and using a land cover raster for each winter field season, we calculated class-level landscape metrics for each individual's winter use area with the 'landscapemetrics' package in R, an extension of FRAGSTATS (McGarigal 1995, Hesselbarth et al. 2019).

## Survival Analysis

Using encounter histories for ruffed grouse collected for this study (2020-21) and data collected previously during the winters of 2015-17 (Shipley et al. 2020), we constructed known fate models in Program MARK to estimate weekly winter (Nov – Mar) survival of ruffed grouse (White and Burnham 1999). We used a recurrent time horizon based on a biological calendar of winter starting on 1 November and ending on 28 March (Fieberg and DelGiudice 2009). Winter field season was treated as a grouping variable (Winter

Season 1 = 2015/16; Winter Season 2 = 2016/17; Winter Season 3 = 2017/18; Winter Season 4 = 2020/21; Winter Season 5 = 2021/22). Only birds which survived > 7 days after trapping were used in analysis to reduce bias from elevated mortality rates due to trapping-related stress or injury (Pollock et al. 1989). When a mortality signal was detected, we assumed that death occurred at the midpoint between the last day that it was known to be alive and the first day it was known to be dead (Winterstein et al. 2001). For individuals that survived multiple field seasons, we only used the first season of data to avoid bias from censoring individuals in subsequent seasons due to high collar failure after longer than 1 year of deployment.

We used an extension of the staggered entry Kaplan-Meier estimator to estimate weekly survival as it does not assume constant survival for the duration of the study and can be extended to incorporate individual covariates, such as color morph, with a link function (Pollock 2002, Gutiérrez et al. 2003). To test the effect of winter weather and habitat on survival, we developed separate sets of *a priori* models of weekly grouse survival, corresponding to predictions about the independent effects of intrinsic traits (e.g., age and sex), snow and temperature, and habitat on overwinter survival of grouse (Morin et al. 2020). We ranked and selected models in each set using Akaike's Information Criterion corrected for small sample size (AIC<sub>c</sub>; Akaike 1973, Burnham and Anderson 1998). We did not include variables in the same model if they exhibited high collinearity (r > 0.7; Dormann et al. 2013). We first ran a preliminary set of univariate models to test for effects of intrinsic individual traits on survival (n = 87 individuals). Of the models run with individual covariates for sex, age, color morph, and mass at capture, no models contained a beta value that did not overlap zero and the top ranked model (age effect on survival) had an AIC value only 0.75 higher than the null model (Table S1). As such, we did not include intrinsic covariates in subsequent model sets. Our subsequent model sets were run with a sample size of 94 individuals, including 7 individuals with unknown sex.

In our model set exploring the effects of winter weather and phenotypic mismatch on survival, we created weekly time-varying individual covariates by averaging daily values of abiotic weather conditions. Values were spatially averaged across individual winter use areas to represent weekly conditions experienced at the individual level (Fig. 2). We considered models with weekly minimum temperature (°C, average daily minimum temperature) and snow presence or absence (proportion of days in a week where snow depth > 0 cm). To test effects of phenotypic mismatch with snow cover, we constructed a time-varying variable which represented the proportion of days in a week that an individual was phenotypically mismatched with snow cover depending on color morph (i.e., red morph individuals were mismatched during days with snow cover and gray morphs during days with no snow present in their winter use area). We used a common intercept and allowed effect slopes to vary by winter season and considered additive effects of covariates on weekly survival.

We created another set of models to test for the effect of land cover on individual survival using class-level landscape metrics calculated within individual winter use areas. For the Dense Cover, Mature Forest, Clear Cut, and Open cover classes, we calculated proportion of class cover (PLAND), edge density (ED), and mean contiguity index (MCI; Cushman et al. 2008). Landscape metric covariate values were converted to proportions or scaled by 0.01 to match value ranges of other covariates (i.e. proportion of mismatch with snow cover). We created models to test for additive effects of landscape metrics on weekly survival.

Using the covariates from highly supported models ( $\Delta AIC_c < 2$ ) in our winter weather and habitat model sets, we built a unified model set to test our hypothesis that snow cover and habitat characteristics would differently affect red and gray morph winter survival (Morin et al. 2020). To estimate derived weekly survival estimates by morph, we ran the top-ranked model with morph-specific mean covariate values for each morph.

#### Results

Over five winter seasons (November through March; 21 weeks per winter season), we monitored survival of 94 ruffed grouse: 21 in Winter Season 1 ( $n_{red} = 12$ ,  $n_{gray} = 9$ ), 15 in Winter Season 2 ( $n_{red} = 9$ ,  $n_{gray} = 6$ ), 20 in Winter Season 3 ( $n_{red} = 12$ ,  $n_{gray} = 8$ ), 15 in Winter Season 4 ( $n_{red} = 10$ ,  $n_{gray} = 5$ ), and 23 in Winter Season 5 ( $n_{red} = 19$ ,  $n_{gray} = 4$ ). We detected 34 mortalities ( $n_{red} = 23$ ,  $n_{gray} = 11$ ) across all winter

seasons. Most mortalities were attributed to predation: 18 by raptors, 5 by carnivorans, and 3 attributed to unspecified species. There were 5 mortalities attributed to exposure and 3 unknown causes.

While snow presence or absence varied spatially across Sandhill, snow was present consistently from weeks 9 through 15 across all five winters, with variable onset and snowmelt dates across winters. Snow onset was earliest (week 5) in Winter Season 2 and snowmelt was latest (week 21) in Winter Season 5 (Fig. S1). The total number of days with snow on the ground varied from 80 days in Season 4, 91 days in Season 1, 101 days in Season 2 and Season 5, and 104 days in Season 3. Average daily minimum temperature did not vary statistically between years (ANOVA,  $F_{4.735} = 2.148$ , p = 0.08).

The top-ranked survival model from our final set of models indicated that winter survival varied among years (Fig. 3B). The mean derived survival was lowest during Winter Season 2 (S = 0.41; 95% CI: 0.24 – 0.59), and during other seasons, mean survival ranged from 0.55 (95% CI: 0.35 – 0.73) during Winter Season 4 to 0.85 (95% CI: 0.61 – 0.95) during Winter Season 3 (Fig. 3B).

In our first candidate model set testing the effect of phenotypic mismatch and winter weather on grouse survival, the two top-ranked models included a common intercept and phenotypic mismatch for each winter season (Table 1). During Winter Season 2 (the season with lowest overall survival), phenotypic mismatch was associated with lower survival ( $\beta = -1.54$ , SE 0.52), but parameter estimates of mismatch for other years had confidence intervals which overlapped zero. The next top-ranked model contained phenotypic mismatch and minimum temperature, although the 95% confidence interval for minimum temperature overlapped zero ( $\beta = 0.018$ , SE 0.03), and was likely an uninformative parameter (Arnold 2010). Together, these top-ranked models carried 66% of the cumulative model weight (Table 1). Models containing parameters for snow cover or color morph, without accounting for phenotypic mismatch, were not competitive (Table S2).

Table 1. Model selection results for the effects of phenotypic mismatch, snow cover, and minimum temperature on ruffed grouse overwinter survival. Phenotypic mismatch (MM) with snow cover is present in both top-ranked models, supporting our hypothesis that mismatch is an important driver of survival. Variables below include MM1 – MM5 (weekly time-varying individual covariates of mismatch for each winter season, i.e., the proportion of days in a week an individual is phenotypically mismatched with the snow cover), and Min. Temp. (mean daily minimum temperature). All values were averaged spatially over individual winter use areas and time-varying values were averaged temporally by week. Models ranked by AIC<sub>c</sub> (Akaike's Information Criterion, corrected for small sample size).  $\Delta AIC_c$  represents the difference between the topranked model in the candidate set, wis the model weight, and k is the number of parameters. Only models within 2  $\Delta AIC_c$  of the top-ranked model and the intercept-only model are shown.

Survival Model	k	$AIC_{c}$	$\Delta AIC_c$	w
MM1 + MM2 + MM3 + MM4 + MM5	6	317.27	0.00	0.46
MM1 + MM2 + MM3 + MM4 + MM5 + Min. Temp.	$\overline{7}$	318.80	1.53	0.21
Intercept – only	1	322.00	4.74	0.04

In our second model set considering habitat features, we found weak support for models of survival with land cover metrics. All top-ranked models were within 2 AIC<sub>c</sub> of the intercept-only model and the top-ranked model had only 21% of the cumulative model weight (Table 2). We found a modest negative effect of Open habitat on survival, where confidence intervals overlapped zero slightly ( $\beta = -1.43$ , SE 0.81). We also found a modest effect of higher survival in Mature Forest cover, where the confidence interval overlapped zero slightly ( $\beta = 1.44$ , SE 0.75). Parameters for proportional cover of Dense Cover contiguity, and Dense Cover edge density were also present in top-models, but 95% confidence intervals overlapped zero. Models which included an effect for proportion of habitat with Dense Cover were not well-supported (Table S3).

Table 2. Model selection results for the effects of land cover on ruffed grouse overwinter survival. All models were within  $2\Delta AIC_c$  values of the intercept model. Variables below include % Mature Forest and % Dense Cover (proportions of mature forest or dense cover classes), Dense Cover Contig. (dense cover

contiguity index), and Dense Cover Edge (edge density of dense cover). All values were averaged spatially over individual winter use areas and time-varying values were averaged temporally by week. Models ranked by AIC<sub>c</sub> (Akaike's Information Criterion, corrected for small sample size).  $\Delta$ AIC<sub>c</sub> represents the difference between the top-ranked model in the candidate set, w is the model weight, and k is the number of parameters. Only models within 2  $\Delta$ AIC<sub>c</sub> of the top-ranked model and the intercept-only model are shown.

Survival Model	k	$AIC_{c}$	$\Delta AIC_c$	w
$\% \mathrm{MF}$	2	320.03	0.00	0.21
% Open	2	321.15	1.11	0.12
DC Contig. $+$ % MF	3	321.32	1.28	0.11
DC. Contig.	2	321.81	1.78	0.08
% MF + DC Edge	3	321.83	1.79	0.09
% MF + $%$ DC	3	321.95	1.92	0.08
Intercept - only	1	322.00	1.97	0.08

In our final model set testing mismatch, winter weather, and land cover metrics on survival, the model with mismatch varying by winter season and proportion of Open habitat had the most support with 32% model weight (Table 3). All competitive models contained mismatch effects varying by winter season and collectively held 96% of the cumulative model weight (Table S4). In our top-ranked model, phenotypic mismatch lowered survival (primarily during Winter Season 2) (Table 4). During Winter Season 2, weekly survival from the top-ranked model varied by color morph throughout the season (Fig. 3A). When snow cover was present on the landscape (week 5 - 19), gray morphs had higher average weekly survival of 0.98 compared to 0.92 for red morphs. Conversely, when no snow was present, red morph individuals experienced lower mismatch and had higher weekly survival estimates (Fig. 3A). The top ranked model also indicated that high proportions of Open habitat negatively impacted survival throughout the winter season (Table 4). Across the entire 21-week period each winter season, derived survival estimates varied across the years (Figure 3B) with lowest during Season 2 (S = 0.41; 95% CI: 0.24 - 0.59) followed by Season 4 (S = 0.55; 95% CI: 0.35 - 0.73), Season 5 (S = 0.65, 95% CI: 0.48 - 0.79), and was highest during Seasons 3 (S = 0.85; 95% CI: 0.61 - 0.95) and 1 (S = 0.79; 95% CI: 0.58 - 0. 91).

Table 3. Model selection results for the effects of phenotypic mismatch, temperature, and land cover on ruffed grouse overwinter survival. Phenotypic mismatch (MM) with snow cover is included in all top-ranked models suggesting it is an important driver of winter grouse survival. Variables below include time-varying covariates of MM1-MM5 (weekly time-varying individual covariates of mismatch for each field season, the proportion of time in a week an individual is phenotypically mismatched with the snow cover in its winter habitat), and constant covariates for % Open and % Mature Forest and (proportion of Open or Mature Forest cover, respectively). All values were averaged spatially over individual winter use areas. Models ranked by AIC<sub>c</sub>(Akaike's Information Criterion, corrected for small sample size).  $\Delta$ AIC<sub>c</sub> represents the difference between the top-ranked model in the candidate set, w is the model weight, and k is the number of parameters. Only models within 2  $\Delta$ AIC<sub>c</sub> of the top-ranked model and the intercept-only model are shown.

Survival Model	k	$AIC_{c}$	$\Delta AIC_c$	w
MM1 + MM2 + MM3 + MM4 + MM5 + % Open	7	314.36	0.00	0.32
MM1 + MM2 + MM3 + MM4 + MM5 + % MF	7	315.31	0.94	0.20
$\dots$ Intercept – only	1	322.00	7.64	0.01

**Table 4.** Parameter estimates from the overall top-ranked known-fate model of ruffed grouse overwinter survival at Sandhill. The effect of phenotypic mismatch with snow cover varied by winter field season suggesting that mismatch is variably important for determining overwinter survival. Percent of habitat covered by open habitat also had a negative effect on overwinter survival. The model included a common

intercept, Mismatch1 – Mismatch5 (weekly time-varying individual covariates of mismatch for each field season, the proportion of days in a week an individual is phenotypically mismatched with snow cover) and % Open (a constant covariate for proportion of individual use area covered by Open habitat).

Parameter	Beta	SE	Lower $95\%$	Upper $95\%$
Intercept	4.34	0.36	3.64	5.04
Mismatch1	0.78	0.84	-0.87	2.43
Mismatch2	-1.64	0.52	-2.66	-0.62
Mismatch3	1.53	1.14	-0.71	3.77
Mismatch4	-0.92	0.62	-2.12	0.29
Mismatch5	-0.29	0.59	-1.45	0.87
% Open	-1.98	0.86	-3.66	-0.31



Figure 3. Winter survival estimates by color morph from the top-ranked model for ruffed grouse over five winter seasons. The negative effect of phenotypic mismatch with snow cover was strongest during the second winter season of the study, when overall survival estimates were lowest. (a) Derived weekly survival estimates during the second winter field season in 2016-17, gray shaded area indicates the period of persistent snow cover and (b) derived overwinter survival estimates by color morph over five winter seasons (Nov – Mar, 2015-18 and 2020-22). The top-ranked model included time-varying individual covariates of mismatch and proportion of winter use area covered by open habitat. Mean covariate values by morph were used. Error bars are 95% confidence intervals.

## Discussion

We predicted that phenotype-by-environment interactions between color morph and snow would drive differences in survival within and among winter seasons. We further predicted that phenotypic mismatches would vary across winter with gray morphs exhibiting higher survival during period of persistent snow cover and red morphs having higher survival during times with little or no snow cover. We found that phenotypic mismatch with snow explained differences in survival between ruffed grouse color morphs throughout the winter season, but the magnitude of the mismatch effect was variable across years. Specifically, phenotypic mismatch had the highest impact during the winter with lower overall survival. During this winter, weekly survival flip-flopped across morphs with red morphs having higher weekly survival during snow-off periods (the beginning and end of the winter season) and gray morphs having higher weekly survival during snow-on periods (the core of the winter season).

For many species, cryptic coloration is a critical adaption for evading predation and depends on both the visual ability of the predator and the prev matching a background environment characterized by a suite of factors such as light conditions, ground substrate, and land cover (Cott 1940, Endler 1990, 1992, Stevens and Merilaita 2009). In high-latitude ecosystems, seasonal snow cover transforms the physical environment and can have strong implications for the survival of cryptically colored species through increased predation risk during times of phenotypic mismatch. We found evidence in some years of our study that phenotypic mismatch with snow cover reduced survival throughout the winter season for ruffed grouse, potentially through the same mechanisms found in other species of reduced background matching leading to higher predation for phenotypically mismatched individuals (Zimova et al. 2018, Wilson et al. 2019, Koskenpato et al. 2020). Although grouse are subject to high predation rates from a diverse suite of avian and mammalian predators, grouse populations across the Upper Midwest appear to be most vulnerable to raptors in winter (Small et al. 1991, Shipley et al. 2020), which have higher visual sensitivity compared to mammalian predators such as covotes and humans (Endler 1993, Stevens and Merilaita 2009). We observed this in our study where the majority (76%) of mortality events were attributed to predation and more than half (69%)of those predation events were attributed to raptors. Previous research into the dynamics of northern forest prey communities suggests increased abundances of one species may alleviate predation pressure on other prey species, as was seen for North American porcupines *Erethizon dorsatum* through an experimental revival of a snowshoe hare *Lepus americanus* population (Wilson et al. 2022). Interestingly, the predominantly avian predator guild for ruffed grouse may decouple grouse from this system, despite grouse and have mortality both being dictated by mismatch-mediated predation pressure. Regardless of color morph, the mottled and disruptive coloration patterns of ruffed grouse plumage, which may provide increased camouflage in forest habitats with variable light conditions, indicates that selection for camouflage is an important driver of ruffed grouse coloration (Endler 1993, Rusch et al. 2020). Our results suggest that the persistence of red and gray color morphs reflects a further adaption of increased crypsis to match with seasonal snow cover. Consequently, the presence of multiple morphs within a species could be an adaptation strategy of "bet hedging" that favors the survival of one morph over another during certain environmental conditions (Xue et al. 2019).

In addition to cryptic coloration, thermoregulatory properties associated with coloration have been proposed as an alternative or complementary function for polymorphic and seasonally color changing species in winter environments. For example, winter white pelages in seasonally color changing mammals are more insulative than brown summer coats and further, the winter coats of more northerly snowshoe hare are longer and denser than those of hares in lower latitudes (Gigliotti et al. 2017, Zimova et al. 2018, Kennah et al. 2023). Similarly for a polymorphic raptor, denser contour feather structure has been found in the gray morph of the tawny owl *Strix aluco*, providing increased plumage insulative capacity over red morph individuals (Koskenpato et al. 2016). While we included minimum temperature as a covariate in our weekly survival analyses, we found no strong effect of temperature on survival. Thermoregulatory ability is a function of many different processes related to intrinsic properties such as coloration, behavior, body size, and metabolism, but also many extrinsic properties such as land cover, solar radiation, and weather (Stuart-Fox et al. 2017). Often, color polymorphic traits in birds and mammals are correlated with a suite of other behavioral, sexual, and ecological traits through pleiotropic effects at the loci or other associated genes (Mundy 2005, Roulin and Ducrest 2011). To test whether morphs exhibit different thermoregulatory abilities, more research is needed into the genetics and potential morphological, behavioral, or metabolic differences between ruffed grouse color morphs.

Our findings support our general hypothesis that phenotypic mismatch would predict overwinter survival, but we found that the negative effect of mismatch was not constant throughout the years of our study. The effect of mismatch was strongest in years when overall winter survival was lowest, suggesting that mismatch is important, but the strength of its effect may be conditional on other factors. We did not find any support for general climate conditions mediating survival, and as such, the variability of the mismatch effect may be due to other extrinsic factors such as fluctuations in local predator abundances or availability of quality food resources (e.g., mast or aspen buds). Higher abundances of predators may increase predation pressures on grouse and subsequently increase the importance of phenotypic matching with background to avoid predation. Low food resources or high abundance of chemically guarded aspen buds, an important winter food source for grouse, may in turn lower overall body condition and make individuals more vulnerable to predation (Jakubas and Gullion 1991). Alternatively, snow presence or absence alone did not predict differences in overwinter survival, but differences in snow cover characteristics such as depth and density or fine-scale spatial or temporal variation in these properties may also mediate the effects of mismatch on survival. For example, snow-roosting in deep, low-density snow has been shown to lower stress and increase survival for ruffed grouse potentially by providing concealment from predators and protection from cold ambient temperatures through the insulative properties of deep snow (Shipley et al. 2019, 2020). Limited availability and use of deep, low-density snow for snow roosting during years of low or variable snowfall may increase the effect of phenotypic mismatch on survival. Timing of snow season may also amplify the effect mismatch as the winter season we saw the strongest effect of mismatch was also the year with earliest onset of persistent snow cover (Fig. S1). Alternatively, mismatch may always have a negative impact on survival. but the effect was only detectible in our study sample in years with a high enough number of observed mortalities. Further research into the drivers of morph-specific survival should be explored in areas of their range with different snow regimes and predator assemblages to further disentangle the effects of phenotypic mismatch and winter conditions on survival.

In addition to exploring effects of phenotypic mismatch and weather, we also explored effects of habitat type on overwinter survival for grouse. We predicted that individuals occupying areas of dense cover such as young aspen forest, would have higher survival. Dense cover associated with high stem density such as young aspen forest is thought to provide refuge from predators (Whitaker and Stauffer 2003, Zimmerman et al. 2009). Additionally, we predicted that dense cover may be able to offset negative impacts of phenotypic mismatch on survival, as was found for phenotypically mismatched snowshoe hare (Wilson et al. 2019). Instead, we found increased proportion of open habitat had a negative effect on survival, regardless of morph. Although ruffed grouse tend to occupy a range of different forest types and ages, they are very closely associated with young successional forests and reach highest populations densities in young aspen habitat (Zimmerman et al. 2009, Tirpak et al. 2010). Much of the literature documenting the importance of young forest and dense cover for grouse concerns habitat requirements during breeding and brood rearing seasons. Winter habitat requirements may differ from other seasons in that dense cover habitat is not as important for survival, and instead, survival is lower in landscapes with more open habitats. We suggest that this is driven by low concealment from predators in more open habitat types. Additionally, mature forest cover had a positive effect on survival, potentially because buds of mature aspen trees have been identified as a high-quality winter food source for ruffed grouse (Gullion and Marshall 1968, Doerr et al. 1974).

#### Implications

Our work adds to a growing body of literature on the importance of snow for mediating survival and population persistence of winter-adapted species in northern ecosystems (Petty et al. 2015, Zuckerberg and Pauli 2018, Smith et al. 2022). Phenotypic mismatch with snow presence or absence appears to impact ruffed grouse winter survival and provides a possible explanation for the proposed geographic structuring of morph ratios across the ruffed grouse's range. It has long been speculated that morph ratios in grouse

covary with latitude and snow season length, with higher proportions of gray birds in northern areas and more red individuals in southerly and coastal regions (Bump et al. 1947, Rusch et al. 2020), but there has been no previous work to formally describe the potential mechanisms of these patterns.

Investigating drivers of morph-specific survival differences in color polymorphic species is critical for understanding how species might adapt to novel environmental conditions such as reduced snow cover in a rapidly warming climate. Modern climate change has created and will continue to create novel selective pressures and environmental conditions for species (Parmesan 2006). For many high-latitude ecosystems, and specifically the Upper Midwest, climate change has resulted in earlier snow melt, a reduction in the number of days with persistent snow cover (Choi et al. 2010), and an overall decrease of snow cover extent across the Upper Midwest (Andresen et al. 2014). Climate predictions for the Upper Midwest and Northeastern United States project these trends will continue in future decades (Notaro et al. 2014, Demaria et al. 2016), and pose a significant threat for winter-adapted species (Williams et al. 2015). Understanding how snow cover affects survival for winter-adapted species is crucial to informing conservation decisions as climate change continues to alter snow cover duration and extent (Sultaire et al. 2016, Zuckerberg and Pauli 2018). This is especially true for ruffed grouse, a species experiencing population declines across the Upper Midwest, specifically along its southern range boundary in Wisconsin. Our findings may help inform future conservation actions such as selecting individuals best-suited for translocations or identifying regions in a species' distribution where they may be most vulnerable or resilient to shifting winter conditions (Roulin 2014, Baling et al. 2016, Mills et al. 2018, Smith et al. 2022).

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