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DO INSULATING CHARACTERISTICS OF FEATHERS VARY AMONG COLOR
PHASES IN RUFFED GROUSE (*BONASA UMBELLUS*)?

by

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A Thesis Submitted in Partial Fulfillment
of the Requirements for a Degree with Honors
(Zoology & Wildlife Ecology)

The Honors College

University of Maine

May 2017

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ABSTRACT

Ruffed grouse (*Bonasa umbellus*) occupy a wide distribution in North America, from Georgia in the south to Alaska in the north, as well as southern and central Canada. Color phases in ruffed grouse range from red to gray with gray phase birds found more frequently at higher latitudes than red birds. Gray and red morphs become exclusive at northern and southern range margins, respectively. This pattern is generally attributed to increased ability of gray morphs to survive northern winters. Although a number of mechanisms have been proposed for these relationships, recent studies on tawny owls have suggested that increased feather barb density and proportion of plumulaceous material in gray morphs may provide an adaptive advantage in northern climates due to increased insulation. Our objective for this study was to evaluate if ruffed grouse exhibit similar relationships between insulating feather characteristics and color phase. We collected dorsal and ventral body feathers from live-caught ruffed grouse and supplemented these with samples collected from harvested birds. We quantified feather length, plumulaceous length, and two barb density measurements for each feather using a dissecting microscope. We used generalized linear models to evaluate differences of feather barb density and proportion of plumulaceous material among color phases. We concluded that the models of color phase, as a predictor of barb density and plumulaceous feather material, were not significant. Our results suggest gray phase and red phase individuals have similar feather barb density and proportion of plumulaceous material, inconsistent with the findings for tawny owls, and that insulating characteristics of feathers likely do not contribute to latitudinal gradients of color phase in ruffed grouse.

Dedicated to my loving father, C. Benjamin Keefner, my motivation for completing this work and the man who taught me to problem solve and cope with stress.

December 18, 1961- January 23, 2017

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INTRODUCTION

Polymorphism is defined as the occurrence of more than one distinct, heritable morph within a population, of which the least common cannot be conserved by frequent mutation (Ford 1945). Several processes may drive the persistence of multiple morphs within a species, including sexual selection, environmental variability, and reversible frequency-dependent predation (Blows et al. 2003, Shigemiyama 2004, Gray and McKinnon 2006). Geographic variation is the result of these factors working separately or together on a large geographic scale, and many studies consider geographic variation in a variety of taxa (Hoekstra et al. 2004, Rosenblum et al. 2004). Latitudinal gradients, or clinal variations, are common patterns of such geographic variation, especially for species that exhibit color polymorphism (Bailey 1978, McLean and Stuart-Fox 2014).

Gloger's Rule, a proposed pattern for geographic variation of color, states that within polymorphic species, individuals with greater pigment concentrations persist in more humid climates than individuals with lower pigment concentrations (James 1991). Aside from the use of melanin in the bearded vulture for thermoregulatory purposes, there have been few exceptions to this rule (Margalida et al. 2008). While the mechanisms behind Gloger's Rule are still poorly understood, some have suggested cryptic benefits, thermoregulatory benefits, or defense against parasites (Caro 2013). By definition, polymorphism is heritable and genetic studies have confirmed that the melanocortin-1-receptor (MC1R) locus is the determining genetic marker for melanic polymorphisms in a wide variety of taxa (Hoekstra et al. 2004, Rosenblum et al. 2004, Mundy 2005).

Other studies have compared fitness among individuals of different color morphs. It has been suggested that color polymorphism plays a role in sexual selection and can have an effect on reproductive success (Roulin 2004). The bearded vulture exhibits geographic variation in color polymorphism as an adaptation in response to environmental variability (Margalida et al. 2008). The puffer *Takifugu niphobles* exhibits reversible frequency-dependent predation when feeding on polymorphic prey and, as a result, probability of prey being consumed because of their color phase depended on color phase distribution of the prey population (Shigemiya 2004). Fitness varies among color morphs in almost all cases (Goldstein et al. 2004, Karell et al. 2013, Koskenpato et al. 2016, Svobodová et al. 2016), however in some cases, there are fitness trade-offs among color phases including differences in mate selection, pathogen vulnerability, and offspring survival (Blows et al. 2003, Burt and Ichida 2004, Greenberg et al. 2006).

Latitudinal gradients of color polymorphism are especially prevalent in avian species (*Anthonis melanura* [Bartle and Sagar 1987], *Turdus migratorius* [James 1991], *Passerculus sandwichensis* [Rising et al. 2009], multiple [Bailey 1978]). Screech owls (*Megascops asio*) exhibit a latitudinal gradient in color phase with gray birds farther north and red birds farther south (Mosher and Henny 1976). Mosher and Henny (1976) suggest thermoregulatory structure differences are genetically linked with color phase and lead to differential overwinter survival. The fine structures of body contour feathers are important for insulation, and therefore thermoregulation (Koskenpato et al. 2016). Koskenpato et al. (2016) conducted a study to compare the fine structures of body contour feathers between brown and gray color morphs of tawny owl (*Strix aluco*), which also exhibit latitudinal variation. Their study indicated that gray tawny owls had denser

feather barbules and had feathers with a larger proportion of plumulaceous material relative to contour feather material. These authors suggested that gray tawny owls were more adapted to colder climates in northern latitudes by virtue of the insulation characteristics of their feathers.

Latitudinal variation of ruffed grouse (*Bonasa umbellus*) color morphs has been documented extensively (Aldrich and Friedmann 1943, Snyder and Shortt 1946, Rusch et al. 2000). Ruffed grouse exhibit a wide variety of plumage colors, but these are generally considered to fall within two distinct color phases: red and gray. Gray phase birds tend to be found more frequently at higher latitudes than red birds, and gray and red morphs become exclusive at northern and southern range margins, respectively (Aldrich and Friedmann 1943). Aldrich and Friedmann (1943) and Snyder and Shortt (1946) both used taxidermy specimens of ruffed grouse collected from throughout their range in attempts to explain this latitudinal variation. Aldrich and Friedmann (1943) concluded that distribution of color phase was related to distinct biomes, suggesting that it was correlated with precipitation, humidity, and temperature. Snyder and Shortt (1946) found that color phase frequency was correlated with local climatic conditions, but did not elaborate as to what these conditions were. Gutiérrez et al. (2003) hypothesized that winter weather conditions affect the probability of predation on ruffed grouse of different color phases where red morphs have a cryptic color advantage in the absence of snow and may have evaded predation more successfully than gray morphs. It has also been suggested that ruffed grouse follow Gloger's Rule, but that the likely reason for ruffed grouse color phase distribution has not been empirically supported (Atwater and Schnell

1989). There has not been a study that considers the thermoregulatory feather structure differences among color phases of ruffed grouse similar to those conducted for owls.

Our objective for this study was to evaluate if ruffed grouse exhibit similar relationships between insulating feather characteristics and color phase as demonstrated by tawny owls (Koskenpato et al. 2016). In doing so, we have attempted to fill this gap in ruffed grouse research and add to the literature on color polymorphism. Similarly to Koskenpato et al. (2016), we evaluated two feather structure variables; the proportion of the feather comprised of plumulaceous material and feather barb density (count/cm), which we consider characteristics of feather insulation. We used generalized linear models to examine covariance between color phase and barb density and color phase and proportion of plumulaceous material. We considered covariates that we anticipated would be sources of variability including color phase, sex, age, position of feather on bird, month of collection, collection site, and mass at time of collection. We hypothesized that gray morphs would have greater barb density and greater proportion of plumulaceous material than red morphs, and we predicted color phase would be the strongest predictor of insulating feather characteristics.

METHODS

Field Methods

We collected body feathers from ruffed grouse that were live-caught as part of an ongoing study (Davis et al. 2016). We captured birds in central Maine at the Frye Mountain Wildlife Management Area and the Stud Mill Road commercial forest during April, May, August, September, and October 2014-2016. The Frye Mountain study area was owned by the Maine Department of Inland Fisheries and Wildlife and was located in Waldo County. The Stud Mill Road study area was located in Hancock County and Penobscot County. Both areas were at comparable latitudes (44.482064 for Frye Mountain and 44.97922 for Stud Mill Road). We distributed modified lily traps (Gullion 1965) at these study areas in forests along secondary roads in places where ruffed grouse presence was likely. Because we needed to increase the sample size for red and gray morphs, we supplemented our sample with feathers collected from birds that were harvested by hunters from locations throughout Maine during the annual ruffed grouse hunting season (October-December). We sampled evenly among color phases for harvested birds. We determined age of captured or harvested grouse as adult (>1 year of age) or juvenile (<1 year of age) and sex based on plumage characteristics (Davis 1969), and used a spring balance to record individual mass (g). Ruffed grouse color phase was determined based on the color of the tail fan. We classified ruffed grouse into five color phase categories in the field: red, intermediate, gray, split, and brown, but chose to only use the former three because they were the least subjective and also fit the gray to red continuum most closely (Figure 1). One representative body feather was sampled for

each individual. All capture and handling of ruffed grouse was approved by the University of Maine Institutional Animal Care and Use Committee (protocol number A2014-03-06).

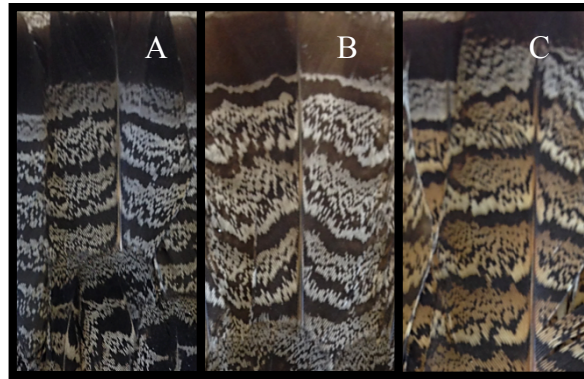


Figure 1. Example depicting three categories of ruffed grouse color phase: gray (A), intermediate (B), and red (C). Feathers were used to evaluate the relationship between color phase and insulating feather characteristics, and were collected from live-caught and harvested ruffed grouse during April, May, August, September, and October 2014-2016.

Lab Methods

We measured feather length (mm) and length of the plumulaceous section (mm) along the rachis of each feather, excluding the calamus (Koskenpato et al. 2016; Figure 2). We marked each feather at the midpoint of the plumulaceous section using a felt tip pen and used a dissecting microscope to count the number of feather barbs within 0.5 cm of this midpoint in each direction; a total feather length of 1 cm (Figure 3). We took two barb counts, one on either side of the rachis, and used the lines on a fixed ruler for guidance to stay within 0.5 cm of the midpoint. We considered the left edge of the leftmost mark on the ruler the start of the 1 cm window and the left edge of the rightmost mark on the ruler the end of the 1 cm window. This precision was necessary to determine whether to count barbs positioned near the edges of the 1 cm window. We processed

feathers in a random order to avoid any bias and classified feathers as dorsal or ventral based on their appearance compared with a reference specimen.

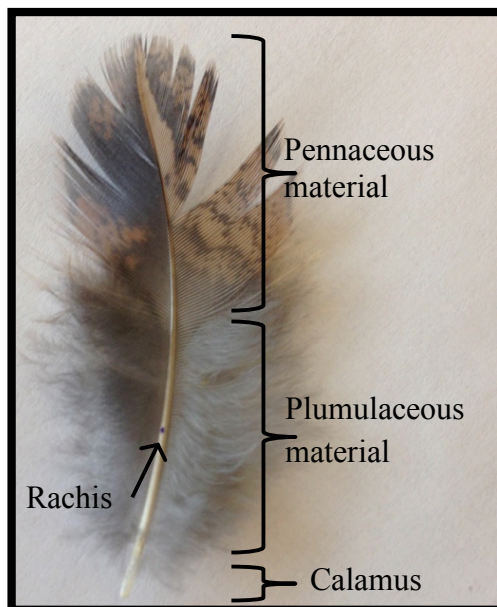


Figure 2. Sections of a ruffed grouse body feather. Feathers were used to evaluate the relationship between color phase and insulating feather characteristics of ruffed grouse.

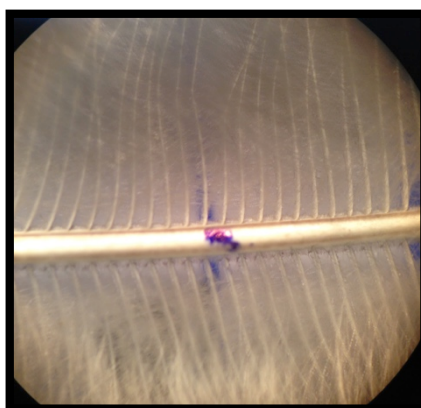


Figure 3. Microscopic view of ruffed grouse feather barbs and point on rachis to mark center of plumulaceous feather material. Feathers were used to evaluate the relationship between color phase and insulating feather characteristics of ruffed grouse.

Statistical Analysis

We used feather measurements to create two continuous response variables that were representative of feather insulation: barb density and proportion of plumulaceous material. We defined barb density as the count of feather barbs per centimeter along one side of the rachis, averaged for our two measurements of each feather. We calculated the proportion of plumulaceous material as the length of plumulaceous material without the calamus (mm) divided by the total feather length without the calamus (mm).

We predicted that color would be the strongest predictor of insulating feather characteristics and that gray ruffed grouse would have greater barb density and greater proportion of plumulaceous material than red birds. We anticipated additional sources of variability might affect insulating feather characteristics and we sought to control for those measures to the extent possible. We considered the effects of age, sex, and mass of the bird, the position of the feather on the bird, and the month and site of capture in both analyses. We also considered length of plumulaceous material as a covariate for barb density because we expected that longer feathers may have inherently lower barb density, but we did not consider barb density as a covariate for proportion of plumulaceous material because barb density is not a predictor of feather length or the length of plumulaceous material.

We predicted the results of some of the potential sources of variation that might have obscured effects of color phase. Adult birds and birds of greater mass are more likely to have body reserves to invest in feather production, so we expected these birds to have longer feathers and, therefore, lower barb density. We anticipated birds caught later in the season would have lower barb density because they would have had more time to

lose barbs from wear. We expected no effect of site on barb density because the main collection sites were at similar latitudes, nevertheless we used site as a covariate in our analysis to test this assumption. Similar covariates were tested for the proportion of plumulaceous material for similar reasons.

We used program R (R Core Development Team 2011) to run generalized linear models (GLMs) with these covariates and contrasted these against an intercept-only null model for both of the insulating feather characteristics. We assessed model support using AIC, where we considered models with AIC scores at least 2.0 less than the null model to be competitive and interpreted beta coefficients as measures of effect size.

RESULTS

We used measurements of one feather from 153 individual birds in our analysis, including 39 feathers from red birds, 68 feathers from intermediate birds, and 46 feathers from gray birds (Table 1). Exploratory analysis of the data suggested an apparent difference in barb density among color phases that was consistent with our predictions (Figure 4), where the mean barb density for gray morphs was 0.7 barbs/cm greater than that of red morphs, and intermediate morphs fell in between. However, the model that included color phase as a predictor of barb density was not considered competitive, with an AIC score 2.6 greater than that of the null model (Table 2), and with beta coefficients indistinguishable from one another. We found that the model with length of plumulaceous material as a predictor of barb density was competitive with an AIC score 45.11 less than that of the null (Table 2). Barb density was negatively related to the length of plumulaceous material (Figure 5).

Dorsal feathers had greater proportions of plumulaceous material than ventral, and feathers from adult birds had greater proportions of plumulaceous material compared with juveniles (Figure 6). We did not consider the models with month and mass as covariates to be competitive because they had AIC scores of only 1.49 and 0.85 less than the null, respectively (Table 3). We also concluded that the model of color phase as a predictor of plumulaceous feather material was not competitive with an AIC score 3.1 greater than that of the null model (Table 3). For both analyses, inclusion of supported variables as additive effects with color phase did not influence support for the color phase effect.

Table 1. Sample sizes for ruffed grouse feathers used to evaluate the relationship between color phase and insulating feather characteristics. Feathers were collected from live-caught and harvested ruffed grouse during April, May, August, September, and October 2014-2016.

Color Phase	Gray	46
	Intermediate	68
	Red	39
Sex	Female	50
	Male	103
Age	Juvenile	72
	Adult	81
Position on Bird	Dorsal	34
	Ventral	119
Site	Frye Mountain	57
	Stud Mill Road	47
	Telos ^a	36
	Western Maine ^a	13
Total		153

^aSamples collected from harvested ruffed grouse.

Table 2. Model selection results for generalized linear models of ruffed grouse feather barb density. Models were built separately for each of the predictor variables. Feathers were collected from live-caught and harvested ruffed grouse during April, May, August, September, and October 2014-2016 (n=153).

Model	Degrees of freedom	AIC	Δ AIC
Plumulaceous Length	3	703.3	0.00
Null	2	748.4	45.11
Position on Bird	3	749.7	46.43
Month	6	749.9	46.60
Age	3	749.9	46.64
Sex	3	750.3	47.04
Mass	3	750.5	47.18
Color Phase	4	751.0	47.68
Collection Site	5	752.3	49.07

Table 3. Model selection results for generalized linear models of proportions of plumulaceous feather material of ruffed grouse. Models were built separately for each of the predictor variables. Feathers were collected from live-caught and harvested ruffed grouse during April, May, August, September, and October 2014-2016 (n=153).

Model	Degrees of freedom	AIC	Δ AIC
Position on Bird	3	-363.6	0.00
Age	3	-334.8	28.78
Month	6	-329.3	34.28
Mass	3	-328.7	34.92
Null	2	-327.8	35.77
Sex	3	-325.8	37.80
Collection Site	5	-325.8	37.80
Color Phase	4	-324.7	38.87

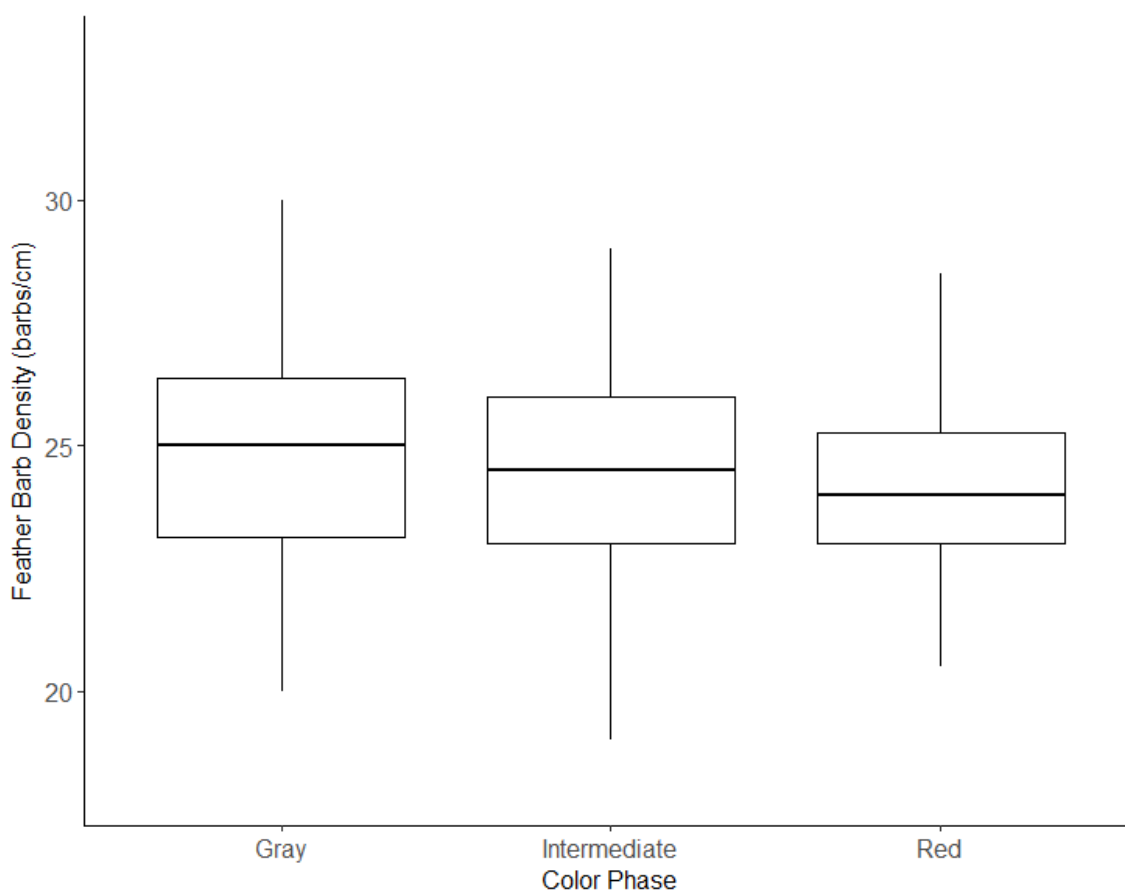


Figure 4. Apparent differences in feather barb density (barbs/cm) among ruffed grouse color phases. The model that included color phase as a predictor of barb density was not considered competitive because its AIC score was greater than that of the null model and the beta coefficients did not vary greatly from one another. Feathers were collected from live-caught and harvested ruffed grouse during April, May, August, September, and October 2014-2016 (n=153).

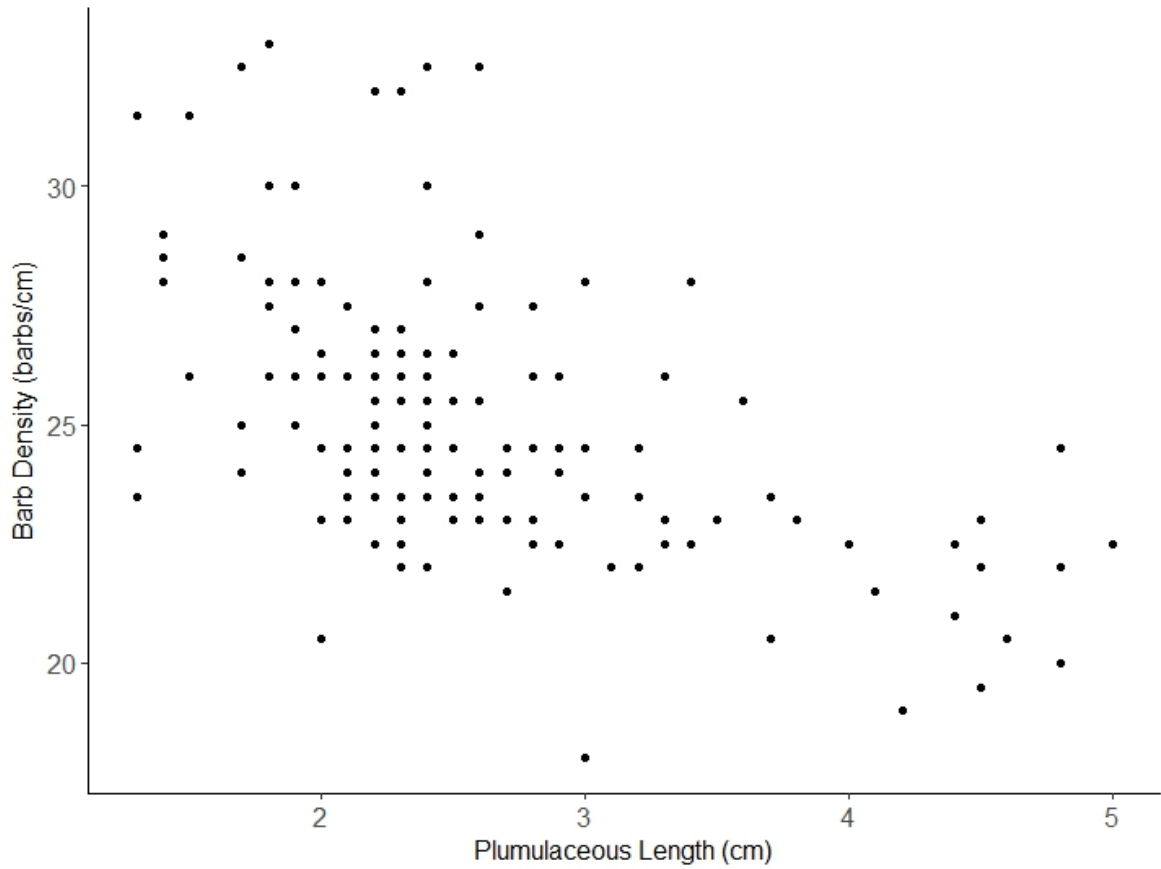


Figure 5. Relationship of plumulaceous length (cm) and feather barb density (barbs/cm) for feathers collected from live-caught and harvested ruffed grouse during April, May, August, September, and October 2014-2016 (n=153).

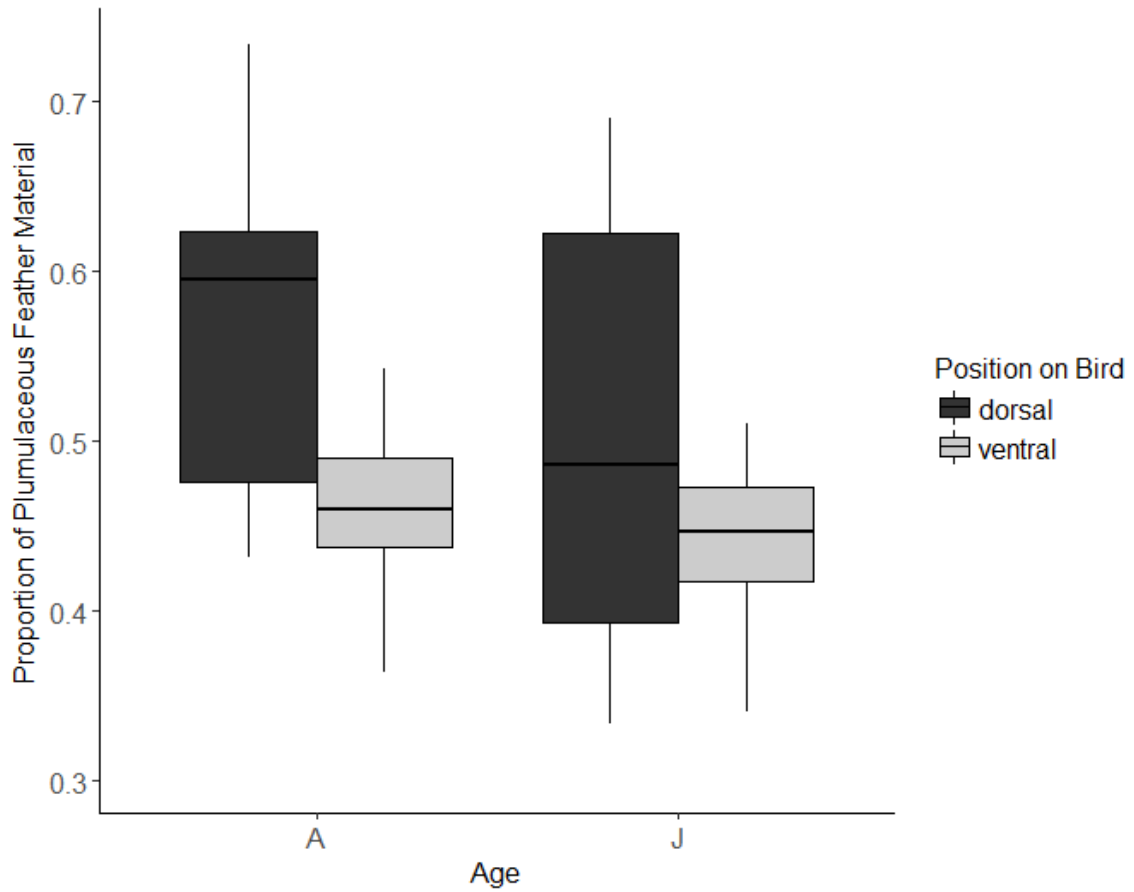


Figure 6. Distribution of the proportion of plumulaceous feather material of each ruffed grouse feather by age (A= >1 year; J= <1 year) and feather position on body. Feathers were collected from live-caught and harvested ruffed grouse during August, September, and October 2014-2016 (n=153).

DISCUSSION

We found that adults had greater proportions of plumulaceous material than juveniles. This result agreed with our predictions, and these findings may be explained because longer feathers had greater proportions of plumulaceous material and larger individuals may have had more energy reserves to invest in growing feathers. The great tit (*Parus major*) also exhibits intraspecific variation in feather coloration as well as variation in proportion of plumulaceous material among individuals, but for the great tit, these differences occur among populations rather than within populations (Gamero et al. 2015). Gamero et al. (2015) found no relationship between coloration and proportion of plumulaceous material for the great tit. We also found that dorsal feathers had greater proportions of plumulaceous material than ventral, potentially because the dorsal side of a ruffed grouse is more likely exposed to the elements.

Although the model of color phase as a covariate for barb density was not competitive, we did find an apparent difference in barb density among color phases of ruffed grouse, and the mean barb density of gray birds was 0.7 barbs/cm more than the mean barb density of red birds. The biological implications of having one additional barb per centimeter of plumulaceous material might be dramatic despite the small effect size of color phase in our study. A ruffed grouse has approximately 4,342 feathers, 557 of which are dorsal body feathers and 595 of which are ventral body feathers (Bump et al. 1947). The average length of plumulaceous material in our study was 2.56 cm. One more barb per centimeter of plumulaceous material on each body feather would accumulate to approximately 2,950 additional barbs over the entire bird.

We did not find a meaningful difference of feather barb density or plumulaceous material among color phases. Despite similar patterns of color phase with respect to latitude between tawny owls and ruffed grouse, our results do not support the hypothesis that color phase of ruffed grouse is related to insulating feather structures similar to the relationship found for tawny owls (Koskenpato et al. 2016). This could be because we lacked sufficient power to detect a relationship even though there was one, or because there is no relationship and other mechanisms are involved.

If there were a relationship between color phase and insulating feather characteristics, we may not have detected it due to insufficient sample sizes. We used simulations to determine the sample size that would be required to detect a difference in barb density among color phases, but even a simulated sample size of 220 feathers per color phase was not always sufficient to identify support for a difference among color phases. Koskenpato et al. (2016) found that proportion of plumulaceous material and barbule density differed between color phases of tawny owls. We considered the proportion of plumulaceous material for this study, but we did not measure barbule density due to time and budget constraints and, as a consequence, may have overlooked a relationship between color phase and insulating feather characteristics, if one existed. Although we found apparent differences in barb density among color phases, based on our data, we cannot conclude that insulating characteristics differed among ruffed grouse color morphs.

The other possibility is that there is no relationship between color phase and insulating feather characteristics and that other mechanisms drive the latitudinal pattern of color phase in ruffed grouse. Thermoregulation from insulating feather characteristics

was one possible explanation for this pattern (Koskenpato et al. 2016), but other explanations include differential success with regards to crypsis (Gutiérrez et al. 2003), thermoregulation related to degree of melanism (Margalida et al. 2008), defense against parasites (Goldstein et al. 2004), and reproduction (Rising et al. 2009). Gutiérrez et al. (2003) hypothesized that winter weather conditions, including snow depth and temperature, affect the probability of predation on ruffed grouse of different color phases where red morphs have a cryptic color advantage in the absence of snow and may have evaded predation more successfully than gray morphs. The bearded vulture exhibits geographic variation in color polymorphism as an adaptation in response to environmental variability with darker birds found in colder areas because the greater pigment concentrations absorb more heat (Margalida et al. 2008). Concentration of melanin was positively correlated with humidity in song sparrows (*Melospiza melodia*) most likely because the concentration of feather-degrading bacteria (*Bacillus licheniformis*) was greater in areas of greater humidity and melanin increases feather resistance to these bacteria (Burt and Ichida 2004; Goldstein et al. 2004). It has also been suggested that color polymorphism plays a role in sexual selection and can have an effect on reproductive success (Roulin 2004).

If an environmental variable is the primary driver of ruffed grouse color phase distribution, a changing climate will surely change this distribution (Møller 2010). We suggest the need for a study that takes color phase into account when comparing fitness of ruffed grouse in a variety of environmental conditions. Our study highlights a gap in the current literature on the understanding of ruffed grouse color phase distribution.

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