Understanding the implications of climate change for birds of the family Phasianidae: incorporating fleshy structures into models of heat dissipation capacity

by

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ABSTRACT

MEGAN LINDSAY SMITH: Understanding the implications of climate change for birds of the family *Phasianidae*: incorporating fleshy structures into models for heat dissipation capacity

(Under the direction of Dr. Richard Buchholz)

Though widespread acceptance of global warming has generated a plethora of studies evaluating the potential responses of species to increased temperatures, until recently, species and genus-specific studies were not common and for many taxa such studies have yet to be completed. One particularly understudied group in this regard is the avian order *Galliformes*. In this study, I focus on the tribe *Phasianidae*. Furthermore, most studies evaluating the potential range changes of species in response to a changing climate fail to account for the ability of organisms to adapt to the changing climatic conditions, either via plastic adaptations or genetic adaptations. Galliformes often have fleshy structures, or bare patches of skin, which may play an important role in heat dissipation and could be of important evolutionary value if the climate continues to warm. Fleshy structures were measured for all species for which images were available using ImageJ, and ranges were characterized by their current and predicted future bioclimatic variables using ArcGIS and range maps available from BirdLife and NatureServe. Models for predicting maximal heat dissipation capacity were modified to incorporate fleshy structures (FS). Multiple regressions were used to evaluate the relationships between FS and bioclimatic variables, and t-tests and Chi-squared tests were used to compare means and nominal data, respectively. I found that ranges will be significantly altered and heat dissipation capacity will be significantly diminished by 2070. Though some evidence supports the

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importance of FS in heat dissipation, this support is equivocal, and the topic warrants further investigation.

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I. Introduction

In this study, I evaluate the potential effects of climate change on phasianids, a family of birds already considered to be of serious conservation concern (Johnsgard 1986, p. xviii). The earth is warming at a rate that could have significant effects on many species, and it is essential that researchers try to understand how species may cope with these changes. The objectives of my study are threefold: a) to understand how climate change will affect the ranges of phasianids, b) to model the role fleshy structures (FS) may play in heat dissipation, and c) to determine how FS may help species respond to climate change.

A. Climate Change and Its Effects

i. What is climate change?

Humanity's effects on the earth's ecosystems are so extreme that we have pushed the earth into a new epoch of unprecedented changes often called the Anthropocene. The Anthropocene is a geological age encompassing the period in which humans have had a significant impact on earth's ecosystem. The Anthropocene may have begun as early as 8000 years ago (Ruddimman 2013), but changes have been most notable since the industrial era.

In particular, humans have had large impacts on the earth's climate system. Over the past century, the climate system has warmed unequivocally (IPCC 2014, p. 1). Several lines of evidence support this unequivocal warming: surface temperatures have increased, the oceans have warmed, and precipitation patterns have changed (Figure 1,

Figure 2). Combined, these lines of evidence support that the global climate is changing rapidly.

Figure 2: Over the past 40 years, there have been continual increases in the total heat content of earth. (This image is licensed under the Creative Commons Attribution 3.0 Unported License.)

Though most agree that climate change is occurring, some policy makers and corporations claim that there is no consensus on humanity's role in global warming (Oreskes 2004). However, according to the IPCC, "It is *extremely likely* that more than half of the observed increase in global average surface temperature from 1951 to 2010 was caused by the anthropogenic increase in greenhouse gas concentrations and other anthropogenic forcings together" (IPCC 2014, p.5). Models that incorporate both anthropogenic factors and natural variation predict warming consistent with the observed trend (IPCC 2014, p. 5). The probability of the observed warming being produced solely by internal forcing is less than five percent (Barnett et al. 2001). This indicates that

neither humans nor natural variation alone are responsible for global warming; rather, both play a role in current climate trends.

Over the past century, the concentrations of greenhouse gasses in the atmosphere have increased. Since 1750 , $CO₂$ concentrations have increased by 40 percent, $CH₄$ levels have increased by 150 percent, and N_2O levels have increased by 20 percent (IPCC 2014, p. 42). Such increases have played a major role in the observed warming. Humans are responsible for the majority of greenhouse gas emissions that have occurred since 1970; specifically, 78 percent of the greenhouse gas emission increase was a result of an increase in $CO₂$ emissions from fossil fuel combustion and industrial processes (IPCC 2014, p. 4). Support for an anthropogenic role in recently observed trends of global warming is strong and should not be ignored.

iii. Predicted impacts on fauna

In 2007 the IPCC named climate change as a potential leading cause of extinctions in the next century. In 2500 studies analyzed, 80 percent of species' changes in phenotype or range were in the direction predicted by global warming (IPCC 2007, p. 112). In general, species are expected to shift their ranges pole-ward and toward higher elevations as a result of climate change (Chen, *et al.* 2011, p. 1024*)*.

Studies have evaluated the realized and potential effects of climate change on a wide variety of species. Chen *et al.* (2011) estimated shifts in species ranges in response to climate change. They found a median shift of 11.0 km per decade to higher elevations, and a median shift of 16.9 km per decade to higher latitudes (Chen *et al.* 2011, p. 1024). Sekercioglu *et al.* (2007) predicted the extinction of 400 to 500 land bird species by 2100. They predicted that an additional 2150 land bird species could be at risk by 2100 (Sekercioglu *et al.* 2007).

However, even closely related species may have drastically different responses to climate change. Several studies have emphasized differences in species responses. For example, for most Antarctic seabird populations more sea ice correlates with greater fitness—particularly, greater survival or higher breeding success. However, emperor penguins (*Aptenodytes forsteri*) may have increased hatching success with less ice, and Adélie penguins (*Pygoscelis adeliae)* in the Ross Sea have increased population sizes with less ice (Croxall *et al.,* 2002). In fact, different populations of Adélie penguins have very different responses to climate change (Croxall *et al.* 2002*).* Peery *et al.* (2012) contrasted responses of three populations of the spotted owl (*Strix occidentalis)* in the Southwestern United States and predicted that each population would respond differently to climate change.

This evidence supports the need for species- and genus-level studies. Such studies are growing in number (see Benning *et al.* 2002; Croxall *et al.* 2002; Davidson *et al.* 2013*;* Hill *et al.* 1999; Hunter *et al.* 2010*;* Midgley *et al.* 2003*;* Peery *et al.* 2012*;* Record *et al.* 2013*;* Reirsten *et al.* 2012*;* Jenouvrier *et al.* 2009*;* Kou *et al.* 2011*;* Kueppers *et al.* 2005*;* Marini, *et al.* 2010*;* McDonald, *et al*. 1992; Sinervo *et al.* 2010*;* Van de Pol *et al.* 2010*;* Wolf *et al.* 2010*;* and Zimbres *et al.* 2012.)

Studies of changes in species ranges predict much more severe declines than paloecological studies have shown occurred in response to past climate change. This may be in part due to the failure of most studies to consider the presence of two options for surviving climate change—(1) relocation to higher elevations or to pole-ward

locations and (2) physical or behavioral adaptations. Reirsten *et al.* (2012) considered the latter by comparing the responses of two morphs of the common guillemot *(Uria aalge*) to variation in the Barents Sea winter sea surface temperature. They concluded that variations in responses between the morphs could lead to microevolution (Reirsten *et al.* 2012). Studies have shown that species change the timing of their life cycles in conjunction with variation in temperature (Chen *et al.* 2011, p. 1024*).* Sinervo *et al.* (2010) considered the ability of *Sceloporus* lizards to adapt to climate change and predicted local extinctions, meaning extinctions from specific habitat patches, to reach 39 percent by 2080. It is essential that studies predicting species' responses to climate change consider the possibility of both relocation and thermoregulatory adaptation.

Physical and behavioral adaptations to climate change may include plasticity or genetic adaptation. Examples of plastic behaviors that could be beneficial to species dealing with warming climates include earlier parturition dates in American red squirrels (*Tamiasciurus hudsonicus*), earlier termination of hibernation in Columbian ground squirrels (*Urocitellus columbianus*), and increased weights of red deer calves (*Cervus elaphus*) (Boutin and Lane 2014, p. 35). Examples of evolutionary responses are more difficult to find, partially because they are more difficult to demonstrate. However, in a study of American red squirrels, advanced parturition date appeared to be heritable and under selection (Boutin and Lane 2014, p. 36). Either type of response—plastic or genetic adaptation—may allow species to cope with increasing ambient temperatures.

B. HDL Theory

I. What is HDL theory?

Without some means of avoiding overheating, animals will experience lower survival under warm conditions to which they are not adapted. Peak temps may result in population bottlenecks. Heat dissipation is an essential component of thermoregulation, but, traditionally, energy has been thought of as a limiting resource, and the ability of animals to obtain energy has been considered the limiting factor on reproduction and survival (Speakman and Król 2010). This way of thinking about energy supply and demand is supported by several lines of evidence. Reproduction tends to coincide with peaks in resource availability (Thomas *et al.* 2001, Daase 2013), and food supplementation has been shown to result in an earlier date of egg laying in free-ranging birds (Davies and Deviche 2014). Additionally, hibernation and migration are both common processes used to avoid periods of reduced food supply (Speakman and Król 2010, p. 727).

More recently, the Metabolic Theory of Ecology (MTE) has been proposed. According to the MTE, metabolic rate controls ecological processes because it limits rates of resource uptake and resource allocation (Brown *et al.* 2004, p. 1771). Metabolic rate can be defined as the overall rate of the processes of energy uptake from the environment, the conversion of energy into usable forms, the allocation of energy to different processes within the organism, and the excretion of metabolic wastes back into the environment (Brown *et al.* 2004, p. 1772). Fundamental to the MTE is the fact that organismal characteristics are controlled primarily by body size, temperature, and chemical composition (Brown *et al.* 2004, p. 1772). The MTE marks a shift in emphasis from a limited amount of energy available to an organism from its environment to a limited energy supply within an organism (Speakman and Król 2010, p. 727).

Specifically, according to the MTE, animals allocate resources to different metabolic needs using a fractional distributional system (Speakman and Król 2010, p. 727). Both MTE and more traditional ways of thinking of energy supply and demand place the limitation on the supply side of the energy equation (Speakman and Król 2010).

Animals experience both periods in which they are constrained by limited resource supply and periods in which they are constrained by intrinsic physiological variables throughout their lives. (Speakman and Król 2010, p. 727). In Hammond and Diamond's peripheral limitation hypothesis, the focus was shifted, for the first time, from a supply side-limited energy balance equation to a demand-limited energy balance equation. According to the peripheral limitation hypothesis, an animal's rate of energy expenditure is limited not by energy supply, but by the metabolic rates of its tissues and organs (Speakman and Król 2010, p. 727). Speakman and Król argue that there is a common factor limiting maximum energy expenditure: the maximum ability of an organism to dissipate body heat; this came to be known as the heat dissipation limit (HDL) theory (Speakman and Król 2010, p. 728).

Numerous lines of evidence support HDL theory. Speakman and Król (2010) explain the origin of the theory in terms of lactation. There appears to be a fundamental limit on lactation; females will increase energy intake when they begin producing milk, but this intake eventually peaks (Speakman and Król 2010). After this peak, manipulations of the litter size, the length of lactation period, and the amount of physical exertion experienced by mothers do not result in increased lactation (Speakman and Król 2010). Attempts to understand this fundamental limit have been elucidating as to the nature of the metabolic limitations that animals face.

An early theory proposed was the central limitation hypothesis, which claimed that the ability of the digestive tract to absorb nutrients limited the maximum energy intake and thus the maximum lactation (Speakman and Król 2010, p. 728). This theory was dismissed when Hammond *et al.* (1994, in Speakman and Król 2010, p. 728) showed that lactating mice subjected to cold temperatures increased their intake of food. This experiment, in conjunction with experiments indicating that mammary glands had a limited capacity, led to the peripheral limitation hypothesis (Speakman and Król 2010, p. 728).

The peripheral limitation hypothesis was in turn dismissed when subsequent experiments by Johnson and Speakman showed that, when exposed to cold temperatures, mice increased milk production (Speakman and Król 2010, p. 728). These experiments support HDL theory because, when the gradient between ambient temperature and body temperature, increases, the ability of animals to dissipate heat also increases. Extreme negative effects of hyperthermia include elevated protein damage, DNA damage in germ cells, liver damage, a disrupted blood brain barrier, and embryonic death in pregnant females (Speakman and Król 2010, p. 729). Hypothermia, on the other hand, has beneficial effects on organisms in many situations (Speakman and Król 2010, p. 729). Therefore, it is logical that animals would be limited by their ability to dissipate heat.

Animals exchange heat at their surfaces primarily through the processes of radiation and convection (Speakman and Król 2010, p. 729). The body can be modeled as if it is composed of two compartments: a central core and a body shell; the temperature of the core is regulated, and the temperature of the shell is unregulated (Speakman and Król 2010, p. 730, Figure 3). Heat is lost through the body surface, where the shell is located,

and the shell provides protection against heat loss (p. 730). Heat loss across the shell (H_s) can be calculated from the thermal conductivity of the insulating layer, the surface area of the organism, the depth of the insulating layer, and the surface temperature of the shell, which is primarily determined by the ambient temperature. Thermal conductivity of the insulating layer, surface area, and depth of the insulating layer can be estimated based on body mass. Thus, body mass and ambient temperature determine the amount of heat that an organism can dissipate. Simplistic modeling using body mass does not usually take into account the role of heads and necks in thermoregulation. Nor does it account for behaviors or physiological attributes that may alter heat dissipation capacity.

Figure 3: The body can be modeled as consisting of a central core that generates metabolic heat and a body shell that insulates against heat loss. Extremities are not normally incorporated in the model calculations.

Climate change is predicted to result in surface warming across much of the globe, though effects will be proportionally greater at high latitudes. When ambient temperatures increase, the ability of organisms to dissipate heat decreases. Therefore, if HDL theory is correct, animals will be more constrained metabolically and will suffer decreases in fitness in response to increasing ambient temperatures. In particular, if the HDL theory is correct, then extreme temperatures, such as the maximum temperature of the warmest month (T_M) , may be a limiting factor in organism survival. Such extreme temperature events may cause organisms to exceed their heat dissipation capacities. Of course, behaviors such as daily torpor or panting may allow organisms to continue to function under such conditions. The understanding of such physiological constraints would benefit from studies incorporating physiological attributes into models of heat dissipation.

C. Study Group

In this study, I focus on the capacity of phasianids to dissipate heat and the potential effects of climate change on this group. The family Phasianidae is in the Order Galliformes. The avian Order Galliformes is a large group consisting of more than 250 species. The group has a nearly worldwide distribution and inhabits a wide range of habitats, including deserts, primary forests, scrub forests, bamboo thickets, cultivated lands, and alpine meadows. Galliformes are chicken-like in appearance, often have elaborate head and neck ornamentation, and may be either monomorphic or sexually dimorphic. They may be sedentary or migratory, but most rarely fly long distances,

preferring to walk. Mating systems vary greatly amongst the group (Johnsguard 1986). Galliformes' wide distribution, relatively high species extinction risks due to climate change, habitat destruction, and human exploitation (McGowen *et a.,* p. 121), and potential to adapt make them interesting subjects for a study of potential climatic change impact.

Galliformes currently face a high risk of extinction, with 26 percent of all galliform species considered at risk, compared to 12 percent of all bird species (McGowan *et al.* 2012, p. 321*).* Of the galliform species listed on the IUCN Red List, 15 percent are considered at risk at least partially due to climate change (McGowan *et al.,* p. 321). Despite this, few studies exist evaluating the responses of Galliformes to climate change, but see R *et al.* (2010), which focuses only on Galliformes in China.

My project focuses on the family Phasianidae, which consists of pheasants, partridges, junglefowl, chicken, quail and peafowl. Phasianidae is broken into the subfamilies Phasianinae and the subfamily Perdicinae*.* The subfamily Phasianinae, the pheasants, consists of non-migratory birds that are terrestrially adapted and moderately large (Johnsgard 1986, p. xvii). Most species are sedentary, may be monogamous or polygamous, and are primarily found in the northern tropics. Their range elevations vary from sea level to approximately 2745 meters. The subfamily Perdicinae includes partridges, francolins, and Old World quail. These birds are non-migratory and are terrestrially adapted. They are generally small to medium in size (Shanaway 1994, p.7).

According to Johnsgard, "of all major bird groups pheasants are among the most seriously impacted by human exploitation and habitat destruction" (1986, p. xviii). Of the 51 species of pheasants included in the IUCN Conservation Action plan, three were

classified as endangered and 21 were classified as vulnerable (Fuller and Garson 2000, p. 7).

Because un-feathered portions of skin, or fleshy structures (FS), are present in many species of Galliformes and vary greatly in size, Galliformes are particularly of interest in respect to the second option for surviving climate change: physical and behavioral adaptations. FS can be simple un-feathered regions on the head and neck, such as ceres, or highly specialized structures, such as combs and wattles (Kimball and Braun 2008, p. 438, Figure 4). They can be smooth or covered in papillae, and coloration varies, though red predominates (Kimball and Braun 2008, p. 438). FS vary widely in size and are often sexually dimorphic.

FS have been considered to be sexual ornamentation, but few studies have considered the costs of FS (Buchholz 1996). FS expose bare skin to temperature extremes, aggressive competitors, and disease-carrying insects (Buchholz 1996). Thus, there must be some adaptive advantage to fleshy structures. FS have often been assumed to be under sexual selection, but there is a lack of association between fleshy ornamentation and other types of ornaments, suggesting that other factors also play a role in selection on fleshy structures (Buchholz 1996). Fleshy structures are highly vascularized, suggesting that they could play a role in heat dissipation. In fact, the unfeathered portions of wild turkeys have been shown to serve thermoregulatory functions when the turkeys are maintained at high temperatures and may enable them to adapt to increased temperatures (Buchholz 1996). The HDL model, however, is a basic biophysical mass-based model that does not consider morphological adaptation for heat

dissipation. Instead it presents a simplistic model that assumes heat dissipation is only dependent on geometric (that is, volume: surface area) biophysical parameters that are calculated based on the body as a sphere or cylinder. To my knowledge, there have been no studies on Galliformes evaluating the potential consequences of such exaptations on climate-induced range shift.

Figure 4: Examples of FS in *Gallus gallus domesticus*. Photo courtesy of Andrew Snyder.

D. Objectives, Hypotheses and Predictions

Hypothesis 1: Climate change will impact the ranges of phasianids.

Prediction a: The maximum temperature of the warmest month (T_M) in species ranges will increase by 2070.

Prediction b: A significant portion of species ranges will cease to be characterized by currently tolerated climatic variables by 2070.

Hypothesis 2: Rising temperatures will threaten the survival of many species of phasianids.

Prediction a: The predicted maximal heat dissipation capacity (max HDC) under current climatic conditions is significantly higher than the HDC predicted under future climatic conditions.

Prediction b: More species will exceed their HDC in future climatic scenarios than do under current climatic scenarios.

Hypothesis 3: Fleshy structures play a significant role in the ability of phasianids to dissipate heat, and could serve as vehicles of adaptation as temperatures rise. Prediction a: The max HDC of most species is significantly higher in calculations that incorporate FS than in calculations that fail to incorporate FS. Prediction b: There is a significant positive relationship between maximum temperature of the warmest month and fleshy structure size.

II. Materials and Methods

A. Compiling data

Species distribution maps for all currently recognized phasianid species were obtained from BirdLife International and NatureServe (2012). *Phasianus versicolor* was omitted from further analyses because no range map was available. ArcInfo grids of bioclimatic variables under current and predicted future scenarios were downloaded from the worldclim database (Hijmans *et al.* 2005). Data on the body masses and altitudinal ranges of species were collected via a literature review conducted by Dr. Richard Buchholz (Buchholz 1997). For species for which there were no values in the literature for altitudinal ranges, occurrence points were downloaded from gbif (The Global Biodiversity Information Facility 2013). Occurrences outside of the species' natural distributions were omitted. If more than 10 points were available, then the minimum and maximum altitudes represented by these points were obtained using a script in R. *Francolinus schlegelii* was omitted from further analyses because less than ten occurrence points were available. A total of 143 species were included in the analyses. Additional species were omitted from certain analyses when data on body mass or FS size were unavailable.

B. Using ArcGIS to determine which bioclimatic variables characterize species current and future ranges

ArcGIS was used to determine which bioclimatic variables characterize the current ranges of species (ESRI 2011). Species distribution maps were limited to include only the portions of the distributions within the altitudinal limits of each species using the extract by mask tool in ArcGIS v. 10.2. Then, the extract by mask tool was used to

determine the ranges of the four selected bioclimatic variables (average annual temperature, mean diurnal range, T_M , and minimum temperature of the coolest month) that characterized the current range of each species. When new rasters were created, it was noted which rasters were converted from 16-bit unsigned rasters to 8-bit rasters, as this altered the values. The copy raster tool was then used to convert these rasters to the original depth (16-bit unsigned), which restored original values. Next, the raster calculator was used on the predicted bioclimatic variables for 2070 to indicate areas where all four of these bioclimatic variables fell into the ranges that characterized areas currently occupied by the species in question. I converted the resulting raster layer into polygons and intersected these polygons with the current distribution polygons to create polygons containing the areas in the current distribution that will continue to be characterized by current bioclimatic variables until 2070. The field geometry tool in ArcGIS was used to calculate the area of the current distribution and of the overlap between the current distribution and the potential future distribution. Finally, the extract by mask tool using current distributions as the mask was used to determine what the T_M would be in the species range in 2070 if the range remained unchanged.

C. Measuring FS Size

Images were obtained from various online databases for each species of phasianid for which images were available. See Appendix A for specific sources. For each species, up to three images of individual males and three images of individual females were obtained where available. For each image, the number of pixels composing the eye, any FS present on the bird, and the body of the bird were measured in ImageJ v.1.47 (imagej.nih.gov/ij). For species with three-dimensional FS, the number of pixels occupied

by the FS was multiplied by the number of exposed sides of the FS. The proportion of the bird covered by FS was calculated, and the surface areas of FS were calculated (Table 1). These measurements were averaged across all individuals available for each gender of each species.

D. Modifying the HDL Equation

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I used the equations developed by Speakman and Król (2010) to predict the heat dissipation capacities of all phasianid species included in the analyses (Table 1). However, the equations used by Speakman and Król fail to account for the head and neck of the birds. Extending these structures may be an important way in which galliforms increase their ability to dissipate heat, so the equation for calculating heat dissipation capacity was modified to incorporate the head and neck (Table 1). Still, fleshy structures are not accounted for in these calculations of heat dissipation capacity. In order to incorporate FS into these calculations, all FS were treated as spheres and the surface area of FS was estimated (Table 1). Due to the wide variation in FS structures, it would have been very difficult to deal with the actual shapes of individual FS. Radiative and convective heat loss through the FS were calculated, and these values were added to the HDC to estimate the HDC when FS were considered (Table 1).

Table 1 Equations used in this study

BM is body mass in grams.

E is Emissivity (0.96) (Tattersall *et al.* 2009).

SB is the Stephan-Boltzman constant (5.6793⁸) (Tattersall *et al.* 2009).

 T_s is the surface temperature of the FS in K, which was considered to be 2 °C less than T_b (Richards 1971).

D is the diameter of the sphere calculated from the SA_{FS} (in meters).

"c" is 0.37, the standard value for a sphere (Mitchell 1976).

"n" is 0.6, the standard value for a sphere (Mitchell 1976).

E. Statistical Methods in R

Excel spreadsheets were used for basic calculations. All statistical analyses were conducted in R version 3.1.1 (R Core Team 2014). The "car", "pastecs", and "ggplot2" packages were used. Welch's Two Sample t-test was used to compare various means. Chi-squared tests were used to compare nominal data.

Multiple regressions were used to determine which factors influence FS size. Variance inflation factor (VIF) scores were calculated to check for collinearity. The average annual temperature was excluded from all models due to a high VIF score. AIC model selection criteria were used to determine the best model. When AIC scores were within two points of each other, the more parsimonious model was chosen (Crawley 2005). Histograms and residual plots were observed to confirm that the assumptions of multiple regression were not violated. Where these assumptions were violated, data were square-root transformed (Field 2012). After transformation, all assumptions were met.

III. Results

A. Climate Change and Species Ranges

Some of my results, but not all, support the hypothesis that climate change will increase the extinction risks to phasianid species. Particularly, by 2070 species ranges will be warmer and a significant portion of species ranges will cease to be characterized by currently tolerated climatic variables.

Currently, the mean T_M is 34.5°C. For 2070, the mean predicted T_M is 36.9°C. The warmest months in 2070 will be significantly hotter than are the current warmest months (t = -3.1825, df = 283.303, p= 0.0016, Figure 5).

Figure 5: A histogram representing the ranges of temperatures that will characterize the warmest months in species ranges under both current and future climatic scenarios.

Figure 6: A boxplot showing the percent increase in T_N between now and 2070. The dark horizontal line represents the median value. The other horizontal lines represent the first and third quartiles. The small circles represent **individual outliers. .**

On average, the T_M experienced will increase by 7.14 percent (Figure 6). The highest predicted percent change is 43.3 percent for the red-legged partridge (*Alectoris rufa*). The red-legged partridge is native to Europe and is categorized as Least Concern by the IUCN Red List, but populations appear to be declining (BirdLife International 2012). For two species, the buff-throated partridge (*Tetraophasis szechenyii)* and Temminck's tragopan (*Tragopan temmincki*) the predicted T_M was lower than the current T_M . The buff-throated partridge is believed to occur in India and China but is rare and poorly known (BirdLife International 2012). The IUCN Red List categorizes this species Example 1.1 and the present increase in 1, between now and 2070.
The dark horizontal line represent the median value. The other horizontal
lines represent the first and third quartities. The small circles represent
indivi

approach the Vulnerable criterion (BirdLife International 2012). Temminck's tragopan is known from the eastern Himalayas up to altitudes of 4575 meters (Johnsgard 1991, p. 116). This species is categorized as Least Concern by the IUCN Red List (BirdLife International 2012).

On average, 63 percent of a species' range will continue to be characterized by currently tolerated bioclimatic variables in 2070 (median = 69.8 , std. dev = 29.4, min = 0, max = 99.7, Figure 7). The variables considered were maximum temperature of the warmest month, minimum temperature of the coolest month, mean diurnal range, and average annual temperature. As expected, significant portions of species ranges will no longer be characterized by currently tolerated bioclimatic variables in 2070 ($z = -2.866$, p $= 0.00209$, Figure 8). For a map depicting an example of what portions of a species range will be characterized by tolerated bioclimatic variables in 2070 see Figure 9. For some species, such as the common pheasant (*Phasianus colchicus*), little to no change in range is predicted. However, for species such as the buff-throated partridge (*Tetraophasis szechenyii)* and the mountain peacock-pheasant (*Polyplectron inopinatum),* range changes of more than 99 percent are expected. The mountain peacock-pheasant is categorized as Vulnerabile by the IUCN Red List (BirdLife International 2012).

Figure 7: A boxplot depicting what percentages of species ranges will continue to be characterized by currently tolerated bioclimatic variables in 2070. The dark horizontal line represents the median value. The other horizontal lines represent the first and third quartiles. The small circles represent individual outliers.

Figure 8: A scatterplot depicting the percent of species ranges that will cease to be characterized by current bioclimatic variables in 2070 categorized based on IUCN conservation status.

Figure 9: Sixty-four percent of the range of *Francolinus bicalcaratus* will continue to be characterized by current bioclimatic variables in 2070. The shaded and hatched areas indicate the entire current distribution of the species. The areas that are hatched indicate the predicted portion of the original range that will be characterized by the same bioclimatic variables in 2070. range that will be characterized by the same bioclimatic variables in

B. Modeling HDC

My results support the hypothesis that rising temperatures will threaten the survival for many species of phasianids. Namely, heat dissipation capacities will be significantly lower in 2070. More, but not statistically significantly more, species will exceed their heat dissipation capacities by 2070.

a. Speakman and Król's equation for heat dissipation capacity

i. For males

As expected, HDC is predicted to be lower in 2070 than it is currently $(t = 2.1247)$, $df = 252.824$, $p = 0.02767$). The mean max HDC when the current T_M is considered is 250.4 kJ/day. The mean max HDC when the predicted T_M in 2070 is considered is 176.5 kJ/day.

Of the 128 species considered, 22 currently exceed their heat dissipation capacities. Of the 128 species considered, 33 are predicted to exceed their heat dissipation capacities in 2070. Contrary to my expectations, the number of species that are predicted to exceed their HDC in 2070 is not significantly greater than the current number (χ^2 = 2.802, p = 0.09415). However, some species will exceed their HDC in 2070 that do not currently. These include the Djibouti francolin (*Pternistis ochropectus*), which is classified as critically endangered by the IUCN Red List (BirdLife International 2012).

ii. For females

The same analyses were performed for females. Again, my results supported my hypothesis that HDC will be lower in 2070 than it is currently $(t = 1.9882, df = 233.665,$

 $p = 0.04796$. The mean max HDC when the current T_M is considered is 227.1 kJ/day. The mean max HDC when the predicted T_M in 2070 is considered is 160.4 kJ/day.

Of the 118 species considered, 22 currently exceed their heat dissipation capacities. Of the 118 species considered, 31 are predicted to exceed their heat dissipation capacities in 2070. My hypothesis that significantly more species will exceed their HDC in 2070 than do currently was not supported (χ^2 = 1.971, p = 0.1603). There is no difference in which species do or will exceed their HDC in males and females; there are two fewer species in which females will exceed their HDC in 2070 than there are in which males will exceed their HDC because there was no information available on the weights of females of these species.

b. Incorporating head and neck

ii. For males

As expected, HDC are predicted to be significantly lower in 2070 than they are currently ($t = 2.2147$, $df = 252.824$, $p = 0.02767$). The mean max HDC when the current T_M is considered is 425.0 kJ/day. The mean max HDC when the predicted T_M in 2070 is considered is 299.6 kJ/day.

Of the 128 species considered, 22 currently exceed their heat dissipation capacities. Of the 128 species considered, 33 are predicted to exceed their heat dissipation capacities in 2070. Contrary to my expectations, significantly more species are not predicted to exceed their HDC in 2070 than do currently (χ^2 = 2.802, p = 0.09415). The species exceeding HDC are the same species that exceeded HDC before head and neck were incorporated.

ii. For females

As expected, HDC are predicted to be significantly lower in 2070 than they are currently ($t = 1.9882$, $df = 233.665$, $p = 0.04796$). The mean max HDC when the current T_M is considered is 385.4 kJ/day. The mean max HDC when the predicted T_M in 2070 is considered is 272.2 kJ/day.

Of the 118 species considered, 22 currently exceed their heat dissipation capacities. Of the 118 species considered, 31 are predicted to exceed their heat dissipation capacities in 2070. Contrary to my expectations, more species are not predicted to exceed their HDC in 2070 than do currently (χ^2 = 1.971, p = 0.1603). Again, the species exceeding HDC are the same species that exceeded HDC before head and neck were incorporated.

C. The Role of FS in Heat Dissipation

The results were equivocal in their support for this hypothesis. Incorporating FS into the model does result in higher predicted heat dissipation capacities in males. However, the correlates of interspecific variation in FS proportion do not support my contention that FS are a widespread adaptation for heat dissipation.

a. Characterizing Fleshy Structures

In order to test this hypothesis, it was first necessary to characterize the FS of phasianids. For males, on average, 0.7878 percent of the body was covered by FS (Figure 10). For females, on average, 0.5772 percent of the body was covered by FS (Figure 10). The green junglefowl (*Gallus varius)* has the largest proportion FS with its FS covering more than 11 percent of the body in males and more than four percent of the body in females

Figure 10: A histogram showing the proportion of body surface area made up of FS in males and females.

b. Incorporating FS into models of heat dissipation capacity

i. For males

As expected, HDC is higher when FS are incorporated into models under current $(t = 2.398, df = 112.23, p = 0.01814)$ and future $(t = 2.0402, df = 109.664, p = 0.04373)$ climatic conditions. Contrary to my expectations, HDC is not significantly lower when future climatic conditions are considered than when current climatic conditions are considered (t = 1.7355, df = 125.796, $p = 0.0851$). The mean max HDC when the current T_M is considered is 613.6 kJ/day. The mean max HDC when the predicted T_M in 2070 is
considered is 452.6 kJ/day. Of the 69 species considered, 7 currently exceed their heat dissipation capacities. Of the 69 species considered, 11 are predicted to exceed their heat dissipation capacities in 2070. Contrary to my expectations, significantly more species are not predicted to exceed their heat dissipation capacities in 2070 than do currently (χ^2) $= 1.022$, $p = 0.3120$). Species that do not currently exceed their HDC but are expected to in 2070 include the Rufous-throated partridge (*Arborophila rufogularis)* and Heuglin's francolin (*Pternistis icterorhynchus*), both of which are categorized as Least Concern by the IUCN Red List (BirdLife International 2012).

ii. For females

Contrary to my expectations, HDC is not significantly higher when FS are incorporated into models under current (t = 1.7626, df = 40.46, p = 0.08552) or future (t = -1.5143 , df = 38.487, p = 0.1381) climatic conditions. Additionally, HDC is not predicted to be significantly lower in 2070 than it is currently ($t = 1.0233$, $df = 55.891$, $p = 0.3106$). The mean max HDC when the current T_M is considered is 559.7 kJ/day. The mean max HDC when the predicted T_M in 2070 is considered is 426.6 kJ/day. Of the 31 species considered, three currently exceed their heat dissipation capacities. Of the 31 species considered, four are predicted to exceed their heat dissipation capacities in 2070. Contrary to my expectations, significantly more species will not exceed their HDC in 2070 (χ^2 0.161, p = 0.6882). The common pheasant does not currently exceed its HDC but will in 2070.

B. Correlates of FS variation:

i. For males

Contrary to my expectations, species experiencing higher a T_M generally have smaller FS ($t = -3.133$, $df = 1,122$, $p = 0.002172$, R-squared = 0.07503, Figure 11). The best model for predicting FS proportion in males included only T_M . See Table 2 for a breakdown of the best models.

Figure 11: A scatterplot depicting the relationship between FS proportion and the T_M .

Table 2 The best models for predicting FC proportion in males with AIC scores.

ii. For females

Contrary to my expectations, the best model for predicting FS proportion did not include T_M . Rather, the best model included mean diurnal range and maximum altitude. Mean diurnal range and maximum altitude explain 13.25 percent of the variation in FS proportion (F-statistic = 7.57, $df = 2$, 84, p = 0.0009). Species experiencing a higher mean diurnal range generally have smaller FS ($t = -3.574$, $df = 84$, $p = 0.0006$, Figure 12). Species living at higher maximum altitudes generally have larger FS ($t - 2.588$, df = 84, $p = 0.0114$, Figure 13). See Table 3 for a breakdown of the best models.

Figure 12: A scatterplot depicting the relationship between FS proportion and mean diurnal range.

Figure 13: A scatterplot depicting the relationship between FS proportion and maximum altitude.

Table 3

The best models for predicting FS proportion in females with AIC scores.

Predictor variables	AIC Score
mean diurnal range and maximum altitude	-503.4393
mean diurnal range and T_M	-503.2839
mean diurnal range, maximum altitude, and minimum	
altitude	-501.5384
mean diurnal range, T_M , maximum altitude, and	
minimum altitude.	-501.9007
mean diurnal range, minimum temperature of the	
coolest month, and maximum altitude	-501.4657

IV: Discussion

Many species of phasianids are already considered to be of top conservation concern. My results show that phasianid ranges warm significantly by 2070. Under such changing conditions, it is likely that many species will become more threatened than they are currently, and some species not currently of conservation concern will be threatened by 2070. Conservationists should note which species will experience the most severe changes when setting conservation priorities.

Phasianids are predicted to have significantly hindered heat dissipation capacities by 2070. Species predicted to exceed their heat dissipation capacities will have to either migrate to areas with cooler climates or adapt to warming temperatures. Migration may be difficult for a variety of reasons. Humans have altered landscapes severely. Range fragmentation resulting from manmade modifications to landscapes could prevent species from migrating or could sever connections between potential climatic refugia (Moritz and Agudo 2013). Some species are already occupying the highest possible altitude. The resulting scenario is termed "falling off the mountain." Species can only migrate to a certain altitude before they reach the "top of the mountain." After this point has been reached, to migrate to higher altitudes would require that species move first through a valley, and, then, up a new mountain. Such migration is unlikely to happen. Furthermore, species migrating to higher altitudes will experience reductions in range size due to the conical narrowing of mountaintops.

Therefore, for some species, adaptation will be the only possibility for coping with rising temperatures. Models of heat dissipation capacity that incorporate FS suggest

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that FS can increase heat dissipation capacities. This suggests that FS would be a good vehicle of adaptation for birds coping with higher temperatures.

An unexpected relationship was found between FS proportion and the T_M . Namely, for males there was a significant negative relationship between the T_M and FS proportion. This is the opposite of what I would have expected, if FS and their function in heat dissipation play an important role in determining species ranges. This unexpected relationship could be the result of a tradeoff, as species with FS may be more susceptible to parasite infection than are species without FS. Zamora-Vilchis *et al.* (2012) found a strong positive association between annual temperature and the prevalence of blood parasites. Therefore, there may be a tradeoff between heat dissipation capacity and susceptibility to parasites. This does not necessarily mean that fleshy structures do not play an important role in heat dissipation capacity. Future studies could more effectively evaluate this relationship by incorporating parasite loads explicitly into models. Furthermore, even if current ranges are not limited by the ability of the birds to dissipate heat, it is feasible that this could become a limiting factor as temperatures rise.

It remains feasible that FS could be a vehicle of adaptation to warmer climates. Moritz and Agudo (2013) noted that plasticity could be insufficient to avoid extinction; for evolutionary rescue to occur, key traits must be moderately to highly heritable or potential growth rates of populations must be high. Future studies should focus on elucidating the heritability of these structures if we are to have a better understanding of how they might be adaptive in the face of global warming. FS are sexually selected for large size in numerous *Galliformes,* and if sufficient heritability in FS and genetic

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variation occurs, then mate choice may accelerate adaptation to the thermal constrains of climate change.

In conclusion, my study shows that phasianids will face increased risk of extinction in the future due to rising temperatures and physiological constrains that may prevent birds from tolerating these higher temperatures. Additionally, my study highlights the importance of investigating whether behavioral and morphological adaptations for heat dissipation, such as FS, in determining species-specific susceptibility to climate change. My study documents the potential of FS to serve as vehicles of heat dissipation useful in adaptation in warming climates in a manner that not simply demonstrated by current interspecific variation in the size of combs, ceres, wattles and other FS.

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APPENDIX A

Sources for Individual Images

APPENDIX B

Species-specific information on range changes

