The Comparative Biology of Avian Thermoregulation at High Temperatures

By

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Abstract

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Endotherms, unlike ectotherms, generate metabolic heat to meet their thermoregulatory demands. As homeotherms their body temperature stays within a certain range of body temperature, often higher than the environment. This ability to maintain a biochemically optimal body temperature bestows protection against unfavourable thermal conditions for endotherms. The energetic costs associated with thermoregulatory metabolism and the limits for thermoregulatory capacity will, however, still set a boundary upon the range and duration of conditions that are tolerated by an endotherm. Especially within the context of global climate change, the effect of ahistorically high ambient temperatures on endotherms will depend heavily on the cost the new conditions will impose upon them. Despite various statistical and mechanistic evaluations of endotherm energy metabolism and heat exchange, these costs and limits are poorly known on the interspecific level. In the first chapter, we review and summarise current understanding of endotherm thermal physiology, identify the unresolved questions and examine the conceptual and methodological challenges to a consensus.

The field metabolic rate (FMR) of an endothermic animal represents its energy expenditure in a natural environment, or its energy budget, and the field water flux of an animal reflects the animal's water requirements. In the second chapter, we examined FMR of 97 avian species and field water flux of 76 species for adults from direct field measurements by the doubly-labelled water (DLW) method, and conducted a phylogenetically informed, comprehensive analysis of the relationship between FMR and field wtaer flux, and multiple environmental and biological variables. FMR was strongly associated with body mass with an allometric exponent of 0.6, and seabirds had lower FMR than terrestrial birds. Birds consuming plant matter had lower FMR compared to omnivores, carnivores or nectarivores, and low ambient temperature was associated with higher FMR. Unlike for BMR, there was scarce evidence for phylogenetic covariance in FMR. Life history traits such as fecundity and migration were also not strongly associated with FMR. Field water flux was strongly associated with body mass with an allometric exponent of 0.6, and seabirds, breeding birds and birds from relatively humid habitats had higher field water flux. There was considerable evidence for phylogenetic covariance, but granivory and mean temperature were not associated with field water flux.

Endotherms maintain a stable body temperature at high ambient temperatures by continuous dissipation of metabolic heat to the environment. This requires endotherms to maintain a balance between heat dissipation and water conservation at multiple temperatures. Birds are relatively small, contain a large amount of metabolically expensive tissue, and are mostly diurnal. As a result, they are severely affected by physiological challenges. In the third chapter, we compiled

evaporative water loss measurements for birds exposed to different temperatures and examined their relationships with ambient temperature, precipitation, diet and circadian cycles. While evaporative water loss at normothermic conditions was associated with precipitation and water content in diet, ambient temperature in their natural habitat was important when birds were exposed to heat stress. Additionally, the circadian cycle had an effect on water evaporation. Active-phase birds that had higher resting metabolic rates lost more water through evaporation than resting-phase birds. The direction and magnitude of relationship between ambient temperature and evaporative water loss at a high temperature also differed between active- and resting-phase birds. These results suggest that birds do not experience a tradeoff between water conservation at lower temperatures and efficient heat dissipation under heat stress, and that the activity level of a bird may affect the ability to dissipate heat through water evaporation.

The upper critical temperature (UCT) of an endotherm represents the temperature that requires it to actively dissipate mettabolic heat through increased energy consumption. Endotherms have relatively low variation in UCT compared to the variation in the lower critical temperature (LCT), but environmental conditions are also linked to intraspecific and interspecific variation in UCT. Difficulty in estimating UCT and differences in data quality complicate the comparative analysis of this variation in UCT. In the fourth chapter, we compiled estimates of UCT for 210 bird species, categorised the information by data quality, and evaluated the relationship between UCT and ambient temperature, precipitation, seasonality, migration and circadian cycle. UCT was positively correlated with maximum temperature in the natural range and negatively correlated with body mass, long-distance migration and summer precipitation. Birds in the resting phase of the circadian cycle had lower UCT compared to birds in the active phase. Including the studies that did not include temperatures well above UCT resulted in slightly reduced coefficient estimates for UCT and thus lower accuracy. However, data quality did not severely impact the precision of estimates.

For Floppy, Oyster and Post

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Chapter 1. Unresolved Questions in Endotherm Thermal Physiology

1.1 The biology of metabolic rates

The metabolic rate of an organism is the rate at which it expends chemical energy(IUPS Thermal Commission 2003). As tissues vary in their energy consumption according to the physiological state of the individual, metabolic rates differ on a continuous scale in accordance with the activity level of an animal. The maximal metabolic rate of an animal may be several times the minimum, or basal, metabolic rate(Swanson 2010), and laboratory measurements may differ considerably from those in the field.

The basal metabolic rate (BMR) is the minimum energy consumed by a resting, post-absorptive, non-reproductive endotherm (McNab 1997), with minimal loss of body heat to the surroundings. While BMR represents idealised conditions seldom observed in the field, making its biological significance controversial, it is relatively easy to measure under standardised conditions, and therefore can be incorporated into interspecific comparative studies. The field metabolic rate (FMR), on the other hand, is the average energy expenditure of an organism under natural conditions. FMR is biologically important as it represents the daily energy requirement for an individual (Anderson and Jetz 2005), but methods that are costlier, less precise and harder to standardise are required for its measurement, such as the doubly-labelled water method (Speakman 1998).

The maximal metabolic rate (MMR) is the maximum energy expenditure of an animal over a short period of time (McKechnie and Swanson 2010). Animals are exposed to physical exertion that leads to exhaustion, and their oxygen consumption is determined by respirometry. This value is closely related to the maximum thermoregulatory energy consumption, as shivering thermogenesis produces heat by muscular activity. Equipment such as treadmills (e.g., Bundle et al. 1999, Ellerby et al. 2003), running wheels (e.g., Chappell and Dlugosz 2009, Dlugosz et al. 2012) and wind tunnels (Bernstein, Thomas and Schmidt 1973) have been successfully utilised in the measurement of maximal metabolic rates, but they cannot readily be used on wild-caught individuals, rendering information on endotherm MMR relatively scarce.

The association between metabolic rates and various morphological, physiological and ecological characteristics of endotherms has been the topic of an ongoing debate. As it is difficult to standardise the measurements for field and maximal metabolic rates, basal metabolic rates have been the most extensively examined. In this section, current academic understanding of the biology of metabolic rates will be summarised with a focus on BMR.

1.1.1 The allometry of metabolic rates

A striking property of the metabolic rate is that it scales in relation to body mass(Calder 1981). The relationship is not linear but loglinear with a slope less than 1. Larger animals expend larger amounts of energy, but smaller animals require larger energy expenditure per body mass. Kleiber (1932) had led a pioneering study on allometric scaling, examining heat exchange through the surface of an animal’s body and the mechanical energy of fluids moving through circulatory networks as potential mechanisms. The relationship between body mass and metabolic rate is found across taxa and at both resting and active animals, but the scaling exponent is not universal(White, Cassey, and Blackburn 2007). Mechanistic models have therefore been proposed to address metabolic scaling, often based either on surface area relationships or on circulatory networks (but see Agutter and Tuszynski (2011) on the possibility of biochemical mechanisms underlying allometric relationships).

Models focusing on surface area relationships argue mainly that exchange of energy and matter depends on the surface area of an organism. As the surface area is related through a power law to the volume, it follows that exchange of matter and energy will have a power-law relation to the volume of the organism. The loss of heat to the atmosphere (Roberts, Lightfoot and Porter 2010, Speakman and Krol 2010) has been proposed as a mechanistic basis of surface area relationships at the cellular level, while others put an emphasis upon the exchange of matter (Kooijman 1986, Glazier 2005) for larger cells and at the organismal level.

The West, Brown and Enquist (1997) model, on the other hand, places the circulatory network as the basis of allometric relationships. This model postulates that resource distribution is a major energetic cost that has been optimised through evolutionary history. This evolutionary constraint leads to structural similarities in circulatory networks and to the scaling of the cost of transport according to size. This model has been extended to intracellular networks (West et al. 2002) and to systems without inherent fractality in circulatory networks (Banavar et al. 2010). Combined with temperature dependence of biochemical reactions, this model has been extended to the ecological scale (Brown et al. 2004).

However, models with a single, universal mechanism for allometric scaling show more discrepancies with existing data compared to more complex models. Assumptions for models focusing on circulatory networks are unrealistic in that the evolutionary optimisation of energetic costs for transport is poorly supported (O'Connor et al. 2007). The model also does not agree with data from animals with smaller body sizes (Savage, Deeds and Fontana 2008). Incorporating differences between functional tissues and energy reserves (Maino et al. 2014) allows these models to address the role of surface area relationships (Shestopaloff 2016).

Contrary to the expectations from a mechanistic model of a single underlying process, the scaling exponents of the relationship are also dissimilar across taxa. In mammals the exponent is approximately 2/3 (White and Seymour 2003), while metabolic rates scale with a power closer to 3/4 when multiple taxa are examined (Savage et al. 2004). This exponent has a significant phylogenetic signal (Capellini, Venditti and Barton 2010), and although it is associated with endothermy (White, Cassey and Blackburn 2007) and body mass (Packard and Birchard 2008), it cannot be reduced to consistent morphological differences (Isaac and Carbone 2010). This heterogeneity is insensitive to different statistical methods (Sieg et al. 2009), and the degree of heterogeneity across taxa also differs in birds and mammals (Rezende et al. 2002, McNab 2016). An information-theoretic approach (White, Frappell and Chown 2012) also supports the use of multiple allometric exponents.

The allometric scaling of the metabolic rates of active animals has only recently been examined. A scaling exponent of 0.67 similar to that of BMR has been proposed for the field metabolic rates of endotherms (Hudson, Isaac and Reuman 2013, but also see Packard 2017 for an alternative interpretation). Processes that increase energy demands, such as lactation (Douhard et al. 2016) and exertion (White et al. 2008, Dlugosz et al. 2013), elevate the scaling exponent, and the exponent is higher at higher metabolic rates. Mechanisms such as the aerobic capacity of muscular tissue driving the high metabolic rate (Weibel et al. 2004), increased mechanical resistance from the transportation network (Barbosa et al. 2005) and heart rate (Hedrick, Hancock and Hillman 2015) contribute to allometric scaling. It is likely that the relative contribution of these mechanisms will change as metabolic demands increase (Darveau et al. 2002, Glazier 2008).

Thus, while the allometric scaling of metabolic rates is a universal phenomenon, it cannot readily be reduced to a single mechanism that dominates energy metabolism. Instead, various mechanisms at the molecular, cellular and organismal level link the metabolic rate with the body size of an animal. A comprehensive understanding of the mechanism of the allometric scaling of metabolic rate, however, still remains to be achieved.

1.1.2 Biological significance of the basal metabolic rate

Animals spend a significant proportion of time either in a non-resting state or in a temperature range that requires additional thermoregulatory energy expenditure. Due to the relative ease of standardised measurement, BMR is most commonly used to represent energy consumption of endotherms. However, unlike FMR as the energy expenditure of an animal in its natural habitat, BMR cannot be directly interpreted as a biologically meaningful variable.

Similarly to field metabolic rates (Anderson and Jetz 2005), basal metabolic rates are closely associated with environmental conditions. Comparative studies of basal metabolic rates both within and across species (e.g., Cooper and Gessaman 2004, McNab 2016) reveal consistent trends of higher BMR in areas of lower ambient temperature (e.g., Broggi et al. 2007, Jetz, Freckleton and McKechnie 2008, Nilsson et al. 2011, Luna, Naya and Naya 2017), higher latitude (Wiersma et al. 2007), and greater seasonality (Cavieres and Sabat 2008), while endotherms in tropical areas (Londono et al. 2015), deserts and arid climates have low BMR (Tieleman and Williams 2000, Withers, Cooper and Larcombe 2006). Seasonal variation in BMR is also influenced by environmental conditions (Maldonado et al. 2012, Noakes, Wolf and McKechnie 2017). It is possible that these factors influence BMR through resource availability; habitat productivity (Bozinovic et al. 2009), insularity (e.g. Noakes et al. 2013) and habitat quality (Gutierrez et al. 2012) have been found to affect BMR. Especially in birds, for which primary productivity is not closely associated with BMR (White et al. 2007), it is also possible that thermoregulation by generation of metabolic heat at low ambient temperatures results in higher BMR for cold-adapted species(Fristoe et al. 2015).

Although these patterns do not warrant the functional significance of BMR, the connection between BMR and fitness has been addressed by several hypotheses. The two best-characterised hypotheses are the performance, or increased-intake, hypothesis and the allocation hypothesis. The performance hypothesis (Bennet and Ruben 1979) postulates that the basal metabolic rate of endotherms evolved in conjunction with a high metabolic performance, and that high basal metabolic rates are linked to a larger energy budget. The allocation hypothesis (Deerenberg et al. 1998) proposes that there is a hard upper limit on the total energy budget. The animal therefore experiences a trade-off between thermoregulation and other biological needs such as activity, growth and reproduction. As basal metabolic rates are heritable (Ronning, Moe and Bech 2005) independently of the heritability of body mass (Ronning et al. 2007, Tieleman et al. 2009), the evolution of basal metabolic rates in endotherms is also closely tied to the relationship between BMR and biological functions.

1.1.2.1 Physiological performance

Endothermy has evolved independently in birds and mammals, which leads to various postulates on the adaptive value of a higher metabolic rate that led to endothermy. Endothermy allows for sustained physiological activity at a wider range of ambient temperatures, but it is not clear if this advantage had been sufficient to confer higher fitness to early endotherms, as the constant expenditure of energy for basal metabolism combined with a relatively small thermoregulatory ability is likely to have lowered fitness. Therefore, the link suggested by the performance hypothesis between high BMR and various measures of the physiological performance of endotherms is a key to understanding the evolutionary origin of endothermy. Evolutionary hypotheses on the origin of endothermy therefore focus on finding a link between high basal metabolic rates and various measures of the physical performance of endotherm, in line with the performance hypothesis between basal metabolic rates and physiological performance(e.g., Hayes and Garland 1995, Clarke and Portner 2010).

The 'aerobic capacity' hypothesis (Bennet and Ruben 1979) suggests that the evolution of endothermy is linked to the fitness benefits of an increased rate of oxygen consumption in physical activity. According to this hypothesis, a higher maximal metabolic rate is connected to metabolically costly tissues required for exertion and therefore an increase in BMR. Interspecific comparative studies suggest positive correlation between basal and maximal metabolic rates (e.g., Swanson et al. 2012, Nespolo, Solano-Iguaran, Bozinovic 2017), but intraspecific studies do not universally support this hypothesis. Correlations between BMR and MMR between individuals are context-dependent (Careau et al. 2014). More active individuals do not have higher BMR, and BMR does not always increase when activity levels are empirically adjusted (e.g., Deerenberg et al. 1998, Careau et al. 2013). Plastic changes in basal and maximal metabolic rates do not coincide (Lu, Zhong and Wang 2007), and artificial selection experiments yielded mixed results on the association between BMR and MMR (Sadowska et al. 2015, Wone et al. 2015).

Another set of hypotheses concerning the evolution of basal metabolic rate connects BMR to metabolically expensive processes. The maintenance of certain tissues, such as the digestive tract, liver and reproductive structures, requires high energy consumption. This maintenance cost results in higher metabolic rates with increased investment on these tissues. In some mammalian (Sadowska et al. 2013) and avian (Barcelo et al. 2016) species, high activity in the digestive tract coincides with a high metabolic rate. Investment on reproductive tissue has been also suggested as a possible factor on the evolution of metabolic rates (Koteja 2000, Farmer 2000), although lactating mice did not show an association between investment in milk production and resting metabolic rates (Speakman and Krol 2004). Interspecifically, the masses of various metabolically expensive tissues, such as the heart, liver, kidneys and testes, were related to basal metabolic rates (Wiersma et al. 2012).

The association between low ambient temperatures and high BMR suggests a role of thermogenic capacity in the evolution of BMR in endotherms. The obligatory heat hypothesis (Naya et al. 2012) suggests that thermogenic needs exert a selective pressure on basal metabolic rates. An animal’s rate of heat loss to ambient temperature determines the amount of metabolic heat required to maintain its body temperature setpoint. As expected from this hypothesis, harsh winters promote higher survival for individuals with higher BMR (Nilsson and Nilsson 2016). The degree of seasonal plasticity in BMR is also connected to environmental conditions (e.g., Versteegh et al. 2012, Cortes et al. 2015), suggesting an association between higher BMR and elevated thermogenic needs.

1.1.2.2 Life history

Life histories may be defined as a suite of different strategies that affect survival and reproduction (Ricklefs and Wikelski 2002). The number of combinations of strategies present in nature, however, is much smaller than is theoretically possible, with trade-offs between survival and reproduction and between longevity and fecundity. Highly active species with higher growth rates and larger investment into reproduction, also referred to as the ‘fast-living species’, are often shorter-lived. ‘Slow-living species’ that are generally sedentary, slow-growing species with low fecundity have longer lifespans. A fast pace of life requires high activity in the metabolically expensive tissues also associated with higher BMR. Thus, a connection between basal metabolic rate and the pace of life has been suggested (McNab 1980) and extensively examined.

If a high basal metabolic rate is connected to a 'fast' pace of living, species and populations with higher metabolic rates will demonstrate higher rates of growth and senescence. Interspecific comparative analysis in birds generally supports this prediction. Passerine species with higher BMR demonstrate faster growth as nestlings (Ton and Martin 2016), and neotropical birds have slower growth rates compared to temperate species (Jimenez et al. 2013a), a relationship maintained at the cellular level (Jimenez et al. 2013b). Lower BMR is correlated with longer incubation times and higher investment in innate immunity (Pap et al. 2014). On the other hand, age of maturity and growth rate were not correlated with the metabolic rates of mammals (Lovegrove 2009). Intraspecific studies of birds also suggest that individual variation in metabolic rates do not predict the rates of senescence in birds (Bowhuis et al. 2011, Ronning et al. 2014), investment in immunity (Versteegh et al. 2012), or the production of reactive oxygen species, a group of highly active oxygen-containing compounds (Beamonte-Barrientos and Verhulst 2013).

Another trait closely linked to the pace-of-life syndrome is the reproductive output and investment. When reproductive investment was empirically increased by brood size manipulations, increased BMR and the ratio of BMR/FMR was observed (Nilsson 2002). In certain rodent (Boratynski and Koteja 2010) and bird (Ronning et al. 2015) species, overall reproductive success was correlated to higher basal metabolic rates, suggesting that intraspecific differences in basal metabolic rates are connected to differential reproductive investments. A comparison between two closely related rodent species showed that the species that experience larger population fluctuations, often also linked to higher investment into reproductive rates, had higher BMR (Kurta and Ferkin 1991). However, intraspecific comparisons between different dog lineages suggest that this association may be reversed by artificial selection and is not mechanistically tightly connected (Jimenez 2016). Interspecific comparative studies (e.g., Trevelyan, Harvey and Pagel 1990, Speakman 2005, Bech et al. 2016) do not suggest any association between basal metabolic rates and life history traits.

1.1.2.3 Food habits

The food habits hypothesis (McNab 1986, McNab 1988) connects food habits and metabolic rates of animals. It suggests that an animal’s food habit determines the amount of energy that can be obtained from dietary intake, and therfore limits the metabolic rate possible for the animal. According to this hypothesis, animals that consume easily digested matter with low secondary metabolite content available throughout the year will have a larger energy budget and BMR. McNab (1986) suggested that this difference in the energy availability will lead to a higher biological performance and reproductive output.

The food habit hypothesis, however, has only received mixed support. Animals fed low-energy diets develop lower BMRs (Cruz-Neto and Bozinovic 2004, Maldonado et al. 2012). In natural populations of passerine and non-passerine birds, populations with access to high-energy diets have higher BMR (Sabat et al. 2009, McClelland, McKechnie and Chown 2016). However, this correlation is not universal (Bozinovic, Munoz and Cruz-Neto 2007), and artificial selection experiment toward a low-energy diet resulted in a higher BMR (Sadowska et al. 2009). The food habit hypothesis is not universally supported by interspecific, comparative studies. Diet and metabolic rates were related in rodents and carnivoran mammals, (Munoz-Garcia and Williams 2005, Naya et al. 2013), but not in birds (Schleucher and Withers 2002, Sabat et al. 2010) and bats (Cruz-Neto, Garland and Abe 2001). Therefore, whether there is a relationship between BMR and food habits, and whether the relationship conforms to the expectation that BMR is limited simply by energy availability, remains an open question.

1.1.2.4 Behaviour

The performance and allocation hypotheses lead to strikingly different predictions on the association between metabolic rates and behavioural characteristics. The performance hypothesis predicts that animals with a high BMR will display high activity and energy requirements. On the other hand, the allocation hypothesis predicts that individuals with higher BMR will have less energy available for other activities and will demonstrate a relatively low activity level and lower fitness than low-BMR individuals.

Animal personalities, or behavioural syndromes, refer to consistent individual behavioural differences (Sih, Bell and Johnson 2004). Individuals of many species may be categorised into more proactive or more reactive personality types(Careau et al. 2008). Proactive individuals are more exploratory toward novel environments and more frequently involve themselves in risk-taking behaviour. This tendency results in higher energy expenditure for activity. According to the performance hypothesis, proactive individuals have a higher energy budget and greater amounts of costly tissues, thus resulting in high BMR. The allocation hypothesis predicts that active individuals allocate lower amount of energy to BMR. There is a lack of consensus across studies with regards to animal personality and basal metabolic rates. The presence and direction of relationship between metabolic rates and personality types differ among populations (Maldonado et al. 2012) and sexes (Bouwhuis et al. 2013, Sichova et al. 2013), as well as species (Mathot et al. 2009, Lantova et al. 2011, Careau et al. 2015). Therefore, it is likely that basal metabolic rates and animal personality are not directly connected by a single mechanistic pathway.

The establishment and maintenance of high social rank in social animals is energetically costly, and therefore the energy expenditure connected with a high social rank may be examined in terms of the aforesaid hypotheses. In foraging flocks of parids, higher social rank was correlated with higher basal metabolic rates (Roskaft et al. 1986, Hogstad et al. 1987), supporting the performance hypothesis. Bryant and Newton (1994) also reported a slightly higher BMR in dippers of higher social ranks. On the other hand, Vezina and Thomas (2000) and Lewden et al. (2011) reported no significant connection bewteen social rank and metabolic rates. While Senar et al. (2000) reported a higher metabolic rate in siskins of low social ranks, they suggested that this metabolic cost was associated with higher stress levels due to exposure to aggression instead of a result of differences in energy allocation.

It is likely, therefore, that the association between metabolic rates and energy expensive behaviour is not universal. Mechanistic connections between metabolic rates and behavioural characteristics will be necessary to elucidate the exact contexts influencing this relationship. From the observation that positive relationships were present mainly when metabolic rates were measured before behavioural experiments, Biro and Stamps (2010) suggested that higher energy expenditure may lead to increased frequency in costly behaviour. While hormone level is highly variable compared to personality traits or metabolic rates (Holtmann et al. 2017), endocrine pathways affect both metabolic rates and behavioural traits and is a candidate for the mechanistic connection. Stress has been known to alter the connection between metabolic rates and behavioural characteristics (Careau, Buttemer and Buchanan 2013, Killen et al. 2013), further supporting the possibility that endocrine pathways connect these two mechanisms. As corticosteroids influence energy metabolism, behaviour and stress response simultaneously (Careau et al. 2008), they may be a target for further attention. However, these potential mechanisms remain speculative and not empirically tested.

1.2 The biological effects of high ambient temperature

In a postabsorptive resting endothermic animal, tissue maintenance and body temperature regulation are the two main contributors to energy expenditure. Under conditions in which the metabolic heat generated by tissue maintenance is smaller than the amount of heat lost to the atmosphere, the Scholander-Irving model (review in Rezende and Bacigalupe 2015) predicts that the endotherm will generate additional metabolic heat to defend its body temperature. This model is widely accepted in addressing cold tolerance in endotherms.

While endotherms generally increase their metabolic rate in response to high ambient temperatures, the mechanism behind this increase is not as adequately addressed. Increased thermal conductance by the means of evaporation (Rezende and Bacigalupe 2015) and the effect of increased body temperature (Tomlinson 2014) are suggested as the factors that may affect this incrase. However, there yet does not exist a mechanistic model that addresses this increase. Measurements for upper thermal limits are also relatively scarce, and a considerable proportion of the reports rely on statistically unsound measures such as repeated F-tests and fitting by eye. This further complicates the examination of upper thermal limits.

1.2.1 Determinants of the upper thermal limit

As a result of the difficulty in obtaining reliable estimates of the upper thermal limit, there is a relative paucity of literature on the biological and ecological predictors of the upper critical temperature of endotherms. Several studies that address the thermal limits of closely related species, however, provide some insight upon the possible factors associated with upper thermal limits.

Upper thermal limits of endotherms are not strongly correlated with body mass (e.g., McKechnie et al. 2016), unlike their lower thermal limits where larger species are generally more resistant to cold ambient temperatures and unlike in the thermal limits of some ectotherms (e.g., Klockmann et al. 2017). Animals exposed to extreme summer temperatures in natural habitats often demonstrate higher thermal limits than closely related species occupying relatively cool habitats (e.g., Mann 1983, Hayworth and Weathers 1984, Ganey et al. 1993, Cooper and Gessaman 2004). Where the ambient temperature is similar, humidity seems to be a contributing factor of the upper thermal limit; species occupying relatively arid habitats demonstrate higher tolerance to elevated temperatures than more mesic species (Frumkin et al. 1986). Certain ecological characteristics postulated to affect the basal metabolic rate, such as insularity (McNab 2003) and flightlessness (McNab and Ellis 2006) are not associated with thermal limits, indicating that the upper thermal limit is not dictated solely by adjustments in the metabolic rate.

While these environmental factors appear to influence the upper thermal limits of the endotherm, studies encompassing wider ranges of taxa suggest that the variation in upper thermal limits according to their environment is much smaller than that in lower thermal limits (Araujo et al. 2013, Khaliq et al. 2014). From this, they conclude that there is a rigid physiological upper limit on high ambient temperatures which constrain the evolutionary potential for tolerance to heat. The well-documented responses to high temperatures are in accord with such postulates. However, the influence of biological and ecological covariates within this boundary remains to be explored.

1.2.2 Physiological impacts of high temperature

1.2.2.1 Thermal stress

The physiological impacts of thermoregulatory failure on endothermic animals are well-documented at the molecular and cellular level (e.g., Velichko et al. 2013). Abrupt rises in body temperatures are relatively uncommon, and short-term acclimation has been shown to occur in high as well as low temperatures (e.g., van de Ven et al. 2013, Zheng et al. 2013, Swanson et al. 2014). However, certain laboratory experiments (Valencak et al. 2013, Sadowska 2016, but see Ksiazek & Konarzewski 2016) suggest that higher heat dissipation capacity allows for greater physiological activity (Speakman & Krol 2010). When ambient temperatures are high and thermal conductance low, endotherms will exhibit decreased physiological activity. As expected, exposure to high ambient temperature has been documented as a source of decreased biological performance in endothermic species under both field and laboratory conditions.

Not surprisingly, humans are the most extensively studied endothermic species in terms of the possible impacts of high environmental temperature. Mortality from heat waves have long been reported in urban areas (review in Rupa and Samet 2002), with lethal limits as low as 30^{o}C in humid conditions (Mora et al. 2017). The effects of hyperthermia and resulting heat shock are often lethal, and survivors often experience systematic inflammatory responses (Leon and Bouchama 2015), severe reduction in physiological performance and increased mortality (Kovats and Hajat 2008). Elevation in skin temperature due to high ambient temperature results in significantly reduced aerobic performance (Cuddy et al. 2014), and even sublethal heat stress is associated with severe discomfort (Hanna and Tait 2015).

Under laboratory conditions, domesticated and captive endotherms are known to respond to high temperatures by reduced physiological performance. Prenatal exposure of domesticated chickens to high temperatures results in slower assimilation and tissue production and reduced antioxidant enzyme activity (Kamanli et al. 2015). Organismal effects of high temperature in older birds included reduced density of blood cells (Donkoh 1989), reduced exercise performance and growth of muscle cells (Azad et al. 2010), and damage to liver and heart tissue (Chowdhury et al. 2012). Suppressed immune responses as a result of exposure to high temperatures have been observed in domesticated ducks (Marais et al. 2011). Laboratory studies in giant pandas(*Alluropoda melanoleuca*) suggest that relatively large endotherms also suffer reduced performance with elevated temperature (Zang et al. 2017).

Juvenile endotherms with less effective insulatory and thermoregulatory mechanisms compared to those of adults are often severely affected by high temperatures, and exposure to high temperatures affects nest site selection (Tieleman et al. 2008), incubation strategy (AlRashidi et al. 2011) and provisioning decisions (Robertson 2009). Nestling exposure to high temperatures induce reduced growth, inferior body conditions and lower postfledging survival (e.g., Greno et al. 2008, Cunningham et al. 2013, Salaberria et al. 2014, Rodriguez and Barba 2016) as well as direct mortality (Catry et al. 2015). While there are considerable differences across species with regards to nestling response to high ambient temperatures, these effects contribute to the overall negative effects of high temperature on fitness.

Mass mortality can occur as a result of temperatures exceeding lethal thermal limits, typically during heat waves. Prolonged exposure to lethal temperatures have led to deaths in a bat species (Welbergen et al. 2008) and various avian populations (reviewed in McKechnie et al. 2012) in Australia. As extreme climatic events are projected to increase with climate change, and as declining body size, which reduces resistance to temperature extremes, has been observed across multiple taxa (Gardner et al. 2011), it is expected that the cases of mortality in response to heat stress will increase in the future, especially in tropical or subtropical regions where the maximum temperatures are close to thermal limits.

There is some evidence that thermal conditions impose constraints that may induce costs in survival, body condition and reproductive output of adults (Bolger et al. 2005), and that certain species are more vulnerable to sublethal heat stress (Xie et al. 2017). While behavioural adaptations modulate the degree of exposure to thermal stress, thermoregulatory behaviour imposes trade-offs in the time and energy budget of an endotherm. In both birds and mammals, activity is greatly reduced in exposed habitats during warmer hours of the day (e.g., Clark 1987, Zub et al. 2013). A diurnal avian species demonstrated preference of cooler microclimates and reduced movements during periods of high environmental temperature (Carroll et al. 2015). Increased thermoregulatory demands reduce foraging efficiency (du Plessis et al. 2012, Mason et al. 2017). Reduction in parental care behaviour according to thermoregulatory demands has also been reported (Oswald et al. 2008). These trade-offs may interact with other environmental stressors to induce diminished survival and reproductive output (e.g., Gaston et al. 2002).

From the evidence, it is possible to conclude that heat stress results in elevated mortality in addition to reduced physiological performance and reproductive success. However, their combined effects on individual fitness and population dynamics are poorly characterised. Even though it can be expected that reduced body conditions, survival and reproductive success will result in population declines, only one study to this date was able to quantify this connection (Gardner et al. 2016). The role of thermoregulatory challenges posed by high ambient temperatures in the ecological context of climate change impacts remains unresolved.

1.2.2.2 Water stress

Compared to ectotherms, the amount of metabolic heat generated in endotherms is much larger, and the challenge to avoid hyperthermia increases as the ambient temperature approaches body temperature. Under such conditions, evaporation of water is the only efficient mechanism of heat dissipation. As a result, evaporative water loss is minimal at low temperatures, but increases drastically when the temperature gradient between the animal and the surroundings prevents effective heat dissipation by convection (Tomlinson 2016). Evaporation may occur through the skin (cutaneous evaporative water loss; e.g., Marder and Ben-Asher 1983, Munoz-Garcia and Williams 2007) or through the respiratory tract (respiratory evaporative water loss; e.g., Engel et al. 2006). The relative contribution of each pathway varies according to temperature and humidity (Wolf and Walsberg 1996, Williams and Tieleman 2000, Tieleman and Williams 2002) and the presence of specific anatomic or physiological adaptations. Increase in the amount of evaporative water loss is often an important aspect of thermal acclimation (e.g., Marder 1983, Hoffman and Walsberg 1999, McKechnie and Wolf 2004, Sugimoto et al. 2013, Noakes et al. 2016).

Endotherms, therefore, experience a trade-off between reducing the two risks of heat and water stress. As evaporation is the most effective measure of heat dissipation, prolonged exposure to high temperatures result in higher degrees of dehydration (e.g., Salaberria et al. 2014). Adaptations such as countercurrent heat exchange (Schmidt-Nielsen et al. 1970, van de Ven et al. 2016, Danner et al. 2017) allow endotherms to reduce water demands without increasing heat loads. Other species have been reported to conserve water at low humidity(Withers and Cooper 2014, Baldo et al. 2016), possibly through mechanisms such as modulation of membrane lipids (Williams and Tieleman 2005, Munoz-Garcia et al. 2008, Champagne et al. 2016). Animals not adapted to arid climates have also been found to conserve water by reduced cardiac output to appendages (e.g. Zhou et al. 1999) reduced activity of sweat glands (e.g., Baker 1989), and selective brain cooling (Kuhnen 1997, Robertshaw 2006, Hetem et al. 2012, Strauss et al. 2016). At higher temperatures where metabolic heat may not be dispersed by convection or radiation, endotherms are forced to resort to hyperthermia (Taylor 1970, Ostrowski et al. 2003, review in Fuller et al. 2014), which imposes further thermal stress on the animal. Especially for relatively small animals that cannot tolerate hyperthermia, this severely restricts activity (e.g., Mitchell et al. 2009).

As ambient temperatures rise, the need to avoid dehydration and hyperthermia will pose a significant challenge to endotherms. McKechnie and Wolf (2010) predicted that birds will face increased risks of lethal dehydration during the day in subtropical habitats. Albright et al. (2017) postulated similar increases in the risk of lethal dehydration in North America. The challenge of obtaining water is a limiting factor to the most effective heat dissipation mechanism, which is also the only possible pathway of heat loss when the ambient temperature exceeds body temperature. However, these predictions resort to arbitrary lethal thresholds, and it is difficult to disentangle the effects of dehydration and hyperthermia in mortality events. A more mechanistic examination of heat and water balance and of adaptations that conserve water will be necessary to evaluate the validity of these models.

1.2.3 Ecological impacts of high temperature

The thermal niche concept (Porter and Kearney 2009) includes the thermal environment as a component of the fundamental niche of an endothermic organism. The fundamental niche does not evolve quickly along with environmental shifts (Wiens et al. 2010). Under the context of climate change, many endotherms are exposed to suboptimal thermal conditions, resulting in population-wide responses that causes gradual population decline in habitats outside of its fundamental niche.

A large number of studies have examined changes in the geographic range of animals. Birds are more mobile than small mammals and may therefore respond relatively quickly to environmental conditions. In North America (Zuckerberg et al. 2009) and Europe (Chen et al. 2011, Mason et al. 2015), bird populations have demonstrated poleward shifts in their distribution. Bird populations located in climate conditions dissimilar to historical habitats suffered population decline (Stephens et al. 2016). Decline in a ground-dwelling bird species was documented as a response to the combined effects of higher temperature and lower precipitation (Cruz-McDonnell and Wolf 2016) as well as in multiple other avian populations (Pearce-Higgins et al. 2015). Higher spring and summer temperatures were correlated with negative population trends of cold-associated avian species (Pearce-Higgins et al. 2015). These observations support the possibility that climate is an important component of the fundamental niche of an endotherm.

In some cases, ambient temperatures can predict the occurrence and viability of avian populations when the confounding effect of habitat variables are accounted for (Oswald et al. 2011, Stralberg et al. 2009). Thermal environments may influence mammalian as well as avian population dynamics; population declines have been reported in Sierra Nevada ground squirrels despite increases in energy supply (Eastman et al. 2012), and survival in a North American desert kangaroo rat population is negatively associated with diurnal surface temperature (Moses et al. 2011).

On the other hand, despite the large number of studies documenting shifts in population dynamics in response to climate change, studies generally focus on indirect effects of climate change on other environmental variables (Jenouvrier 2013). Species responding heavily to climate change also often does not show low physiological tolerance to heat. Distributional shifts in North American passerines did not match the patterns in climate and did not mitigate temperature changes in their habitat (Currie and Venne 2017). In a high-altitude habitat, negative population trends in birds was not associated with vulnerability to high temperatures (Milne et al. 2015). These findings have led to suggestions that biotic effects are a stronger driver of climate change impacts on population dynamics (Ockendon et al. 2014).

The conflicting evidence with regards to the direct effect of high temperature on population dynamics indicate that the relative contribution of abiotic factors is highly context-dependent, necessiating closer examination of the physiological and ecological characteristics of vulnerable species. Interspecific relationships may interact with physiological tolerance, with more vulnerable species also being less resistant to negative biotic effects (Diamond et al. 2017). The magnitude of indirect climatic effects also depends on the ecological characteristics of the habitat itself (Maron et al. 2015). It is likely, therefore, that any mechanistic connections between population dynamics and thermal physiology will not be sufficiently generalisable without studying particular focal species.

1.3 Methodological concerns in thermal physiology

The detection of ecological patterns in thermal physiology inevitably requires an approach that involves the integration of empirical information across a broad range of space and time. Since the advent of respirometric techniques in the twentieth century, a number of different research groups have tackled the question of determining the heat and water exchange between an endotherm and its environment. However, this accumulation of knowledge was not necessarily accompanied by a methodological consensus among researchers in terms of measurement, reporting and analysis. Even as recent concerns involving the manifold challenges posed by climate change emerge, a large proportion of comparative thermal physiological research is riddled with the need for a standard, efficient method that adequately addresses these discrepancies.

1.3.1 Non-standardised empirical techniques

When the outcomes of multiple studies are compared within a statistical framework, it is of utmost importance that the measurements are methodologically comparable. Multiple sources of discrepancies that result in non-standardised measurements can be found in empirical thermal physiology. Challenges for the researcher include not only the possible issues with experimental set-up and sampling but also the issues that stem directly from the biology of endothermic organisms. It is only relatively recently that many of those concerns have been documented and addressed.

Flow-through respirometry has been widely adopted as a relatively standard and reliable technique to determine the gas exchange and the energy expenditure of an organism (Kristin and Gvozdik 2012). The successful application of this technique, however, may be hindered by interactions between the gases and drying columns (White et al. 2006, Lighton and Halsey 2011) when carbon dioxide production is used to compute energy expenditure (e.g. Whitfield et al. 2015, McKechnie et al. 2016). Sampling regimes within respirometric measurements also influence the outcome (Cooper and Withers 2010). Furthermore, a considerable number of studies have a sample size smaller than three and are possibly influenced by daily or seasonal cycles of metabolic rate (McKechnie and Wolf 2004). Although it has been suggested that the natural variation in resting metabolic rates is not high enough to warrant the necessity of large sample sizes (McNab 2003), a small sample size combined with a lack of documentation on intraspecific variation in thermal physiology is likely to induce biases that are difficult to account for. To prevent these biases from further affecting the accuracy of results, it is recommended that researchers examine the potential error induced by chemical properties of drying columns and collect measurement from at least three individuals(McKechnie and Wolf 2004). Additionally, they must provide accurate information on the sampling regime, time of day, seasonality.

Resting metabolic rates of both ectothermic and endothermic organisms (Nespolo and Franco 2007), including birds (Horak et al. 2002, Versteegh et al. 2008, Broggi et al. 2009) and mammals (Duarte et al. 2010, Boratynski et al. 2017), are repeatable. However, these consecutive measurements have been conducted under relatively similar experimental conditions. The degree of repeatability varies considerably according to experimental settings (Auer et al. 2016) and developmental stage (Lu et al. 2007), suggesting that biological effects cannot be precluded as possible sources of variation in measured resting metabolic rates.

The duration of captivity affects various thermal measurements in endotherms, possibly due to stress responses, although this effect is not constant across species (Larcombe et al. 2007, Cooper and Withers 2012). Animals held in captivity for an extended period of time display changes in basal metabolic rate (Warkentin and West 1990, Thompson et al. 2015) and body temperature (Hilmer et al. 2010). Additionally, even relatively short-term captivity of up to a few weeks has been demonstrated to increase metabolic rates (Swanson and King 2013). This suggests that measurements from long-term captive individuals may not be representative of wild populations, and that it is necessary to record and report the duration of captivity for standardised results.

The order and the duration of exposure to each temperature also influences metabolic responses to ambient temperatures, thus possibly resulting in biases in respirometric measurements. An effect of previous short-term thermal history has been detected in an avian species (Barcelo et al. 2009), highlighting the need to randomise the direction of temperature changes and the order of exposure to temperatures. While a large proportion of empirical studies of energy expenditure determined resting metabolic rates in two hours or less (Downs and Brown 2012), measurement durations ranging between four and ten hours are necessary for birds (Page et al. 2011) and mammals (Cooper and Withers 2009, Connolly and Cooper 2014) to allow the metabolic rate to reach a resting level at the temperatures. Repeated exposure to experimental conditon also decreases stress responses and associated increases in metabolic rates (Jacobs and McKechnie 2014). These concerns must be balanced with the possibility for changes in thermal physiology during captivity, ideally by gathering preliminary information on the effects of captivity.

1.3.2 Missing and incompletely reported data

A necessary pre-condition to a reliable comparative study is that the data are relatively complete and accurately reported. Experimental conditions and sampling schemes vary widely across studies, potentially resulting in a heteroskedastic dataset that necessiates methods of lower statistical power. While an appropriate quantification of uncertainty in the dataset may reduce bias, researchers often concentrate on reporting and discussing the point estimates of thermal variables and neglect the uncertainty in their measurements. Combined with the heteroskedasticity of a comparative analysis, this omission may compromise the precision and accuracy of estimates.

As resting metabolic rates can only be obtained after prolonged exposure to the specific experimental conditions, it is difficult to expose animals to multiple temperatures during a relatively short study period. Frequently, measurements are limited to a small number of experimental temperatures, often in five-degree intervals or larger (e.g. Brush 1965, Mann 1983). The combination of sparse sampling, small sample sizes and a large degree of uncertainty makes it difficult to determine metabolic rates or thermal limits. Most studies report empirical values from simple visual inspection of scatterplots, which makes them unreliable. The relative paucity of literature on endotherm exposure to high temperature (Whitfield et al. 2015) further suggests that a large proportion of reported values are truncated before the upper thermal limit and therefore possibly unsuitable for comparative physiological analysis (Wolf et al. 2017).

Another common problem associated with data quality is the omission of information in literature. As the single greatest determining factor in the metabolic rate of an organism is its body mass, the relationship between thermal biology and the biological and ecological characteristics of a species can only be examined with some information on its body mass. Often, only the range of body masses is reported instead of standard deviation or standard error (e.g., Lasiewski and Dawson 1964, Trost 1972). The sample size is also occasionally omitted (e.g., Marschall and Prinzinger 1991). Furthermore, a considerable number of studies includes only the mean resting metabolic rate and the standard deviation at each temperature without including the individual measured values, even with the advent of online supplementary materials (e.g., Wilson et al. 2011, Bao et al. 2014). Such omissions make it difficult to estimate the degree of uncertainty for the measurements or to re-evaluate the results. Making the raw measurements available in literature along with summaries will prevent further issues concerning the omission of data.

1.3.3 Methodological concerns in statistical analysis

When interspecific comparisons are the focus of a study, the information to be analysed will be phylogenetically correlated to varying degrees. Closely related species will have more similar biological characteristics, and the advent of modern genetic methods has made it possible to obtain estimates of evolutionary relationships that are relatively independent of individual traits (e.g., Jetz et al. 2012). This information on the relative strength of phylogenetic correlation allows the researcher to quantify the expected amount of covariance between traits. While it is beyond the scope of the review to examine every argument concerning the most effective way to incorporate phylogenetic covariance into statistical models, a large number of tools are available, each based on slightly different assumptions about the evolution of biological traits (reviewed in Symonds and Blomberg 2014). These tools are increasingly adopted in comparative thermal physiology (e.g., Reynolds and Lee 1996, Rezende 2001, Nagy 2005). While these methods offer valuable insight upon an important source of variation in physiological traits, the models rely upon linearity and homoskedascity of the residuals, assumptions that may not necessarily automatically hold.

The analysis of thermal variables is further complicated by the fact that a large number of those characters are allometrically related to body mass. Allometric relationships must be logarithmically transformed to be analysed by linear models. It is conventional, therefore, to linearise the relationship by taking the logarithm of the allometrically related values(e.g., Kendeigh 1970, Schleucher and Withers 2002, Hudson et al. 2013). There nonetheless is disagreement on whether this practice induces unintentional biases in the data. Logarithmic transformation weights smaller predictor values against larger values (Packard 2011), leading to the suggestion that nonlinear regression may in some cases be more effective (Packard 2017). Conversely, nonlinear regression underestimates coefficient values at smaller predictor values (White 2011). Examination of allometric relationships in systems other than animal physiology (e.g., Mascaro et al. 2013, Lai et al. 2013) suggests that the bias induced by logarithmic transformation may be relatively small, and that the effect of larger error variances at larger predictor values may be main cause of the bias (Glazier 2011), a problem unresolved by nonlinear regression. The relative magnitude of these sources of bias is associated with the error structure of the data (Xiao et al. 2011), with nonlinear transformation performing better in additive, homoskedastic and normally distributed error. It is likely, therefore, that model choice will benefit from an *a priori* examination of the data and from post-hoc evaluations of model fit (Ballantyne 2013).

Comparative physiology requires the researcher to work with information from non-standardised procedures that vary widely across studies. Studies may have highly heterogeneous numbers of individuals measured and degrees of intraspecific variation. Certain equipment and experimental procedures are more precise and accurate than others, and the time of the day or the time of the year may result in biased measurements. It is possible to introduce some experimental conditions, such as the season, into the analysis as covariates. However, heterogeneity in measurement error and individual variation is seldom addressed. A proposed method introduces individual variation and phylogenetic correlation in both the predictor and the response(Ives et al. 2007), but sacrifices degrees of freedom due to the need to estimate phylogenetic correlation in each biological covariate. Another method is based on a method to correct the estimated coefficients by the degree of individual variation (Hansen and Bartoszek 2012), which also demands the model to estimate a number of additional parameters. Additionally, no currently available software package allows the option to estimate common off-diagonal transformations of the phylogenetic covariance matrix, thus often overestimating phylogenetic signal.

1.4 Concluding remarks

With the projected rise in surface temperature, an understanding of the thermal physiology of endotherms under both normothermic conditions and heat stress is vital to understand the abiotic challenges climate change poses to them. While smaller-scale studies have been able to discover certain connections between thermal physiology and ecology, most connections are specific to certain lineages, certain environments or certain biological contexts. Comparative analysis that incorporates multiple factors across multiple taxa is therefore necessary to achieve large-scale synthesis of this information. However, these attempts have been met not only be the complexity inherent in ecological phenomena but also by methodological concerns that render the collection and analysis of data much more difficult. It is without doubt that inadequate data is preferable to a lack of data. At the same time, it is indisputable that any result will only be as good as the data and the methods adopted in the process. When a massive update of the data is not feasible, the necessary first step toward synthesis of thermal physiology and ecology across multiple levels would be an update of the methodology: any comparative analysis of thermal physiology must take into account the inconsistency and the heterogeneity inherent in the data.

Chapter 2. The environmental and ecological correlates of the avian field metabolic rate and water flux

2.1 Introduction

Throughout the course of its life, an animal is exposed to a variety of physical and biological environments. While laboratory measurements of metabolism and water evaporation provides an understanding of the thermal physiology of an animal under controlled circumstances, the energy and water budget of an animal in the field, also known as the field mteabolic rate (FMR) and field water flux, are related to variation in the animal's environmental conditions and also to its activities. An animal must maintain its food intake for a non-negative energy budget throughout the course of its life in order to sustain itself (Nagy 1987), and a positive energy balance is necessary for growth and reproduction (Kooijman and Lika 2014). Meanwhile, the animal expends water in a variety of physiological activities, and must ingest and metabolically produce an identical volume of water in order to maintain its water balance.

Energy and water expenditure of an animal may be determined in a standardised laboratory environment through respirometry (e.g., Kristín and Gvoždík 2012). The lowest possible metabolic rate for the animal under resting, postabsorptive, thermoneutral conditions, or the basal metabolic rate (BMR), has been suggested to be associated with a number of environmental and ecological variables including ambient temperature (Jetz et al. 2008), seasonality (Cavieres and Sabat 2008), water availability (Tieleman and Williams 2000), insularity (Noakes et al. 2013), life history and food habit (McNab 1980) and behavioural syndrome (Careau et al. 2015), although some of these relationships have been questioned (e.g., Bozinovic and Sabat 2010, Bech et al. 2016). Animals can lower body temperature by cutaneous and respiratory evaporation at the expense of body water (Smith et al. 2017), and animals balance water conservation and thermoregulation according to environmental water availability and temperature through various physiological mechanisms (e.g., Williams 1996, Greenberg et al. 2012, O'Connor et al. 2017). Laboratory studies of water loss through excretion have shown that animals are able to modulate their osmoregulatory physiology according to changes in habitat aridity and water availability in diet (e.g., Fleming and Nicolson 2003, Sabat et al. 2009).

The relationship between energy expenditure of exercising animals and BMR is unclear (Hammond and Diamond 1997, Mckechnie and Swanson 2010), and BMR and FMR of bird species are not closely associated (Ricklefs et al. 1996). Experimental conditions such as humidity that greatly affect water efflux are also often not reported (Gerson et al. 2014), limiting the utility of laboratory measurements of BMR and water flux for predicting FMR and field water flux. Efforts had been made to estimate FMR from BMR and activity budgets (e.g., Weathers and Nagy 1980, Williams and Nagy 1984), but this requires intensive experimental and observational effort.

Field measurements of metabolic rate and water flux by techniques such as doubly-labelled water (DLW) method (Speakman and Hambly 2016) are therefore pivotal to the understanding of water and energy balance in natural environments. Some predictors of the variation in FMR had been examined in previous studies. FMR is allometrically related to body mass with an exponent of 0.67 (Nagy 2005) for endotherms, which is close to the allometric exponent for BMR in mammals (White and Seymour 2003). FMR shows considerable variability across taxa (Nagy et al. 1999, Hudson et al. 2013), and is associated with various environmental and ecological predictors such as ambient temperature and seasonality (Anderson and Jetz 2005), water availability (Nagy et al. 1999), diet (Anderson and Jetz 2005), breeding seasons (Dunn et al. 2018), relative longevity (Møller 2008) and song complexity (Garamszegi et al. 2006). Many of these variables influence both basal and field metabolic rates, the latter by also elevating or lowering the demand for physical and physiological activity in addition to the level of sustenance metabolism. While Anderson and Jetz (2005) provided a relatively comprehensive assessment of the factors known to influence FMR, life history traits such as breeding seasons, pace-of-life syndrome and migratory habits have not been jointly evaluated along with environmental covariates.

There is a relative paucity of comparative studies addressing the environmental correlates of field water flux. Intraspecific differences in field water flux are related to sodium influx (Green and Brothers 1989), and field water flux is relatively greater through the breeding season when the field metabolic rate is also elevated (Doherty et al. 2001). Studies of water balance for fifteen species (Degen et al. 1982) and for emus (*Dromaius novaehollandiae*) in a laboratory condition (Dawson et al. 1983) suggests an allometric relationship between body mass and water flux, but this has not been verified in the field. Interspecifically, granivores have a reduced water flux compared to species consuming foods with higher water content (Tidemann et al. 1989). Desert birds have lower field water flux, alhough this effect is not seen when phylogenetic independent contrasts are used (Tieleman and Williams 2000), suggesting phylogenetic signal in this variable. Overall, there has not been a comprehensive interspecific examination of the factors affecting the field water flux of birds, or those known to influence total evaporative water loss in the laboratory environment.

In this study, we address the effects of ambient temperature and water availability, diet, breeding phenology, pace of life, and migratory habit on the field metabolic rate of birds. We expect FMR to be elevated in birds with higher BMR and in species that engage in higher frequency of costly foraging activity. We predict that habitats of lower ambient temperature and higher water availability will be associated with higher FMR. We also predict that birds with energy-rich diets, a large clutch size and the capability for long-distance migration will have higher FMR, that FMR will be higher for the birds provisioning for nestlings, and that these effects will be preserved even when these predictors are considered jointly.

We also examine the effects of body mass, ambient temperature, water availability, diet and breeding phenology on the field water flux of birds. As water efflux occurs mainly through waste elimination and evaporation, elevated water flux will be associated with an increased need for nitrogen elimination and heat dissipation, and with higher water availability. We therefore predict that habitats of higher ambient temperature and water availability will be associated with higher field water flux. We also predict that dry, protein-poor diets will be associated with lower field water flux, that marine birds will have lower field water flux than terrestrial birds of similar climates due to the higher sodium content in their diet and drinking water, and that higher metabolic demands and heat loads during the breeding season will result in higher field water flux.

2.2 Methods

2.2.1 Data collection

We compiled estimates of the FMR for 104 species from the literature, excluding certain seabirds that spend multiple days in flight overpen ocean, which makes the estimation of daily FMR difficult (e.g., Shaffer et al. 2004), and studies where only juvenile individuals were measured. Relevant literature was collected through Web of Science and Google Scholar using the keywords “field metabolic rate”, “FMR”, “daily energy expenditure” and “DEE”. We retained only the studies with measurements on both FMR and body mass, made in natural or semi-natural conditions, where the birds were allowed to freely fly and forage under exposure to external environmental conditions. For studies that did not present a grand mean of all individuals measured, we used xyscan 4.3.0 (Ullrich 2017) to extract numerical values from the figures within the text. Units of FMR were standardised to be represented as kilojoules per day. For studies where rates of oxygen consumption were presented, a factor of 20.1kJ/LO$_2$ was used to convert to kilojoules (Culik and Wilson 1991). For the one study (Siegel et al. 1999) where only the rate of CO$_2$ consumption was presented, a respiratory quotient was calculated from the content of the bird's diet (Pacheco et al. 2010).

Field water flux estimates were obtained from the literature for 76 species. The measurements from seabirds that spend multiple days in flight over open ocean or from juvenile birds were excluded. Relevant literature was collected through Web of Science and Google Scholar, and the keywords "water flux", "water turnover" and "water balance" were used in the search. Only the measurements made in natural or semi-natural conditions, where the birds were exposed to environmental conditions and were allowed to fly and forage according to its natural diet, were included in the final dataset. Units of field water flux were standardised as grammes per day. For studies where the water flux was reported as a fraction of body mass, we used the reported mean body mass to convert this value to grammes.

We obtained climatic information from the Worldclim dataset (Fick and Hijmans 2017). Dates of study were retrieved from each text, and we used the Zonal Statistics tool on ArcMap 10.2 (ESRI 2013) to identify the mean, maximum and minimum temperature, the mean monthly precipitation, and the precipitation of the driest quarter within 50km radius of the capture location throughout the period of the measurement of FMR. When the mean, the maximum or the minimum temperatures were provided in the study, we used this information. If the duration of the study specified only "summer" and "winter", we recorded the mean and minimum temperatures of the hottest and coldest quarter of the year in the location, respectively. We sampled 500 phylogenetic trees from the dataset provided by Jetz et al. (2012), and averaged these trees using the package phytools (Revell 2012) in R ver 3.4.4 (R Development Core Team 2018).

Biological and life history traits were obtained from multiple sources. When available, we retrieved information on clutch size, clutch number, migration, and diet from the original studies. When the study did not contain information on clutch size and number, we consulted the life history database by Myhrvold et al. (2015) and Handbook of the Birds of the World Alive (del Hoyo et al. 2018). When information on clutch size or number were not available in either of these two databases, we searched Web of Science and Google Scholar using the keyword "breeding", "clutch size", "clutches" and "clutch number" in addition to the scientific name, common name and the synonyms for the common name of the species. Information on food habits and migration were first gathered from the original studies, and then from Handbook of the Birds of the World Alive (del Hoyo et al. 2018). We classified a species as migratory if the location specified in the study included a population that engaged in long-distance migration with distinct breeding and wintering ranges. Most studies noted whether the birds were incubating or were raising nestlings. When the studies were not informative with regard to the breeding status, we matched the dates of the study with the breeding period of the species to determine if the species was breeding or provisioning for nestlings.

2.2.2 Statistical analysis

For potential covariates of the FMR, we used body mass, annual clutch size (clutch size multiplied by annual number of clutches; e.g., Böhning-Gaese et al. 2000), long-distance migration, foraging activity at sea, season of measurement, diet (nectar/plant matter/animal matter/omnivore), breeding period, mean temperature, and mean monthly precipitation as predictors. Mean temperature and minimum temperature were highly correlated (Pearson correlation coefficient = 0.95, $p<0.001$). Because information on mean temperature was more readily available from individual studies, we only used the mean temperature as a predictor. As metabolic rates are allometrically related to body mass (Calder 1981), we log-transformed the FMR and body mass to linearise the relationship. Due to constraints in the sample size ($n=104$)

compared to the number of predictors, we did not include any interactions.

While the covariates that describe interspecific variation in field water flux are not well-known, intraspecific studies suggest that the field water flux of birds is associated with body mass, diet, sodium influx and breeding seasons. We therefore included the body mass, diet, and the breeding period as covariates. Because sodium influx has not been extensively measured, we included a binary covariate for whether the bird is primarily found in marine habitats as a proxy for sodium influx. Seeds have relatively small water content compared to other food materials (Morton and MacMillen 1982), so we included a binary predictor for whether the bird is primarily granivorous. Additionally, the total evaporative water loss of birds is associated with ambient temperature, and birds from arid habitats are known to have reduced water fluxes. Thus, we used the mean temperature during the period of measurement and the precipitation of the driest quarter as environmental predictors. Because the relationship between body mass and evaporative water loss (Williams 1996) and field water flux (Dawson et al. 1983) is allometric, we log-transformed the field water flux and body mass to linearise the relationship. Because the sample size was small (n=76) relative to the number of variables in the model, we did not include two-way interactions.

We analysed the data by PGLS using the package caper (Orme et al. 2013) in R 3.4.4 (R Core Development Team 2018) with the Brownian motion model, and Pagel's lambda was set as the maximum-likelihood value. We evaluated a full model of log(FMR) against log(body mass), annual clutch size, being a seabird, long-distance migration, season of measurement, diet, breeding status, mean temperature and mean monthly precipitation for the field metabolic rates. For the field water flux, we evaluated a full model of log(field water flux) against log(body mass), mean temperature, granivory, precipitation of the driest quarter, being a seabird and breeding period. The full model for each response variable and all nested models were compared by AICc and averaged using the R package MuMIn (Barton 2018).

2.3 Results

2.3.1 Field metabolic rate

Body mass is known to explain the greatest amount of variation in the FMR of birds (Nagy 2005). Accordingly, we compared models containing each predictor in addition to body mass against the base model only containing body mass (Table 2.1). Being a seabird, diet, mean temperature and long-distance migration improved the base model, while phase of breeding, season, annual precipitation and annual fecundity did not.

Model-averaged estimates from a full model comparison suggest that foraging activity at sea, diet, mean temperature and body mass were significant predictors of FMR (Table 2.2). Body mass had the greatest effect size, followed by herbivory and foraging activity at sea (Figure 2.1, Figure 2.2). While comparison of two-predictor models with body mass and an additional variable suggested a significant effect of long-distance migration (Table 2.1), 18 of the 23 seabird species included in the dataset were also long-distance migrants.

The scaling exponent for FMR on the non-logarithmic scale was 0.66. The maximum-likelihood estimate for Pagel's λ from the best model by AICc was 0, with a 95% confidence interval of (0, 0.185), indicating little evidence for phylogenetic covariation.

2.3.2 Field water flux

We compared models containing each predictor in addition to body mass against the base model containing only body mass (Table 2.3). Breeding status, precipitation of the driest quarter, being a seabird and granivory improved the model, while the mean temperature during the timespan of measurement was not informative.

Model-averaged estimates from the full model comparison (Table 2.4) suggest that field water flux is strongly allometrically related to body mass. Non-breeding birds have lower field water flux compared to incubating birds. Seabirds and birds found in habitats with higher precipitation in the driest quarter had higher field water flux compared to terrestrial birds found in arid habitats (Table 2.4, Figure 2.3). The effects of granivory and mean temperature throughout the duration of each study were not statistically significant.

The allometric scaling exponent for field water flux was 0.606. The maximum-likelihood estimate for Pagel's λ from the best model by AICc was 0.648 with a 95% confidence interval of (0.187, 0.927), suggesting the presence of phylogenetic covaration for field water flux.

2.4 Discussion

2.4.1 Field metabolic rate

We found that FMR had an allometric scaling exponent of 0.66. This is lower than the allometric exponent of 0.75 predicted from theoretical models for metabolic rates based on structure of the circulatory network (West et al. 1997) or on surface area-volume relationships (Roberts et al. 2010). Interspecific comparisons suggest that BMR is allometrically related to body mass with a scaling exponent of 0.67 in birds (McKechnie and Swanson 2010) and mammals (White and Seymour 2003). Previous studies of field metabolic rates in birds (e.g., Nagy 2005, Hudson et al. 2013) also suggested an allometric exponent close to 0.67, and Anderson and Jetz (2005) presented an exponent of 0.69 in a study including both birds and mammals.

The maximum likelihood estimate of Pagel's λ suggested a lack of phylogenetic signal. This result contrasts with previous comparative studies on BMR in birds (Rezende et al. 2002, McKechnie and Wolf 2004) and mammals (White et al. 2009), which found significant differences between phylogenetic and conventional multiple regression. Additionally, the summit metabolic rate of birds, which is the maximum metabolic rate in birds undergoing active thermogenesis, is known to be phylogenetically correlated (Swanson and Garland 2009), although the maximal metabolic rate (MMR) by exertion does not appear to be related to phylogeny (Rezende et al. 2002). Our result, however, is in agreement with Anderson and Jetz (2005), who found that phylogenetic and non-phylogenetic analysis did not result in significant differences in the estimates of coefficient value for predictors of FMR. We suggest that FMR is less phylogenetically conserved than BMR, and possibly also that differences in energy budgets associated with activity level, as reflected in the variation in MMR, may account for this discrepancy between BMR and FMR.

FMR was associated with the mean temperature of the habitat. Lower environmental temperature results in elevated BMR across species (Jetz et al. 2008) and across populations (Broggi et al. 2007, Nilsson et al. 2011). Within a population, birds often show elevated BMR in winter (Chamane and Downs 2009) and elevated summit metabolism for active thermoregulation (Liknes and Swanson 1996, van de Ven et al. 2013). The combined effect of elevated levels of BMR and active thermogenesis, in addition to an increase in time spent below the lower critical temperature of the organism, results in a higher FMR. Precipitation, on the other hand, did not have a statistically significant effect, and the effect size was not negative. This is in contrast with some studies ofn BMR that indicate lower BMR in desert endotherms (e.g., Tieleman and Williams 2000, Withers et al. 2006). It is possible that this association was related to a large number of studies having occurred where precipitation was markedly lower during wintertime (Figure 2.S1). However, including seasonality as a covariate did not make this effect statistically significant.

Food habits were associated with FMR. Birds consuming plant matter showed a significantly lower FMR than birds with other diets. Nectarivorous birds had a slightly higher FMR than birds consuming animal or plant matter, and omnivores had a slightly lower FMR than birds consuming animal matter, but these differences were not statistically significant. It has been reported that nectarivores have higher FMR than animals in other dietary categories when the data for birds and mammals are jointly considered (Anderson and Jetz 2005). When the set of study organisms included reptiles, granivores had a lower FMR (Nagy et al. 1999). On the other hand, consumption of plant matter is related to BMR in mammals (Munoz-Garcia and Williams 2005, Naya et al. 2013) but not in birds (Schleucher and Withers 2002, Sabat et al. 2010). Therefore, the difference in FMR may be a product of granivorous birds engaging in a lower frequency of costly activities such as hovering and prolonged flight, not of elevated BMR.

Seabirds had an overall higher FMR than terrestrial birds, in accordance with Nagy et al. (1999). The relatively exposed location of their nests, along with their foraging activity that necessitates longer flights, may increase their energy demands. Seabirds included in this study (e.g., Ballance 1995, Elliott et al. 2013) engage in costly foraging activities such as diving underwater, which is also likely to increase field metabolic rates and energy requirements.

While breeding and provisioning for nestlings is a costly activity, breeding birds did not show an elevated FMR, and FMR was also not related to annual clutch size. Intraspecific studies suggest that brood size is associated with energy expenditure (Burness et al. 2001), due to the increased energy requirement in foraging for a larger number of nestlings. However, because breeding occurs mainly in spring and summer when there is a lower demand for thermogenesis, some intraspecific studies have found that FMR was lower in the breeding than in the nonbreeding season (Doherty et al. 2001). Fecundity is a component of the slow-fast continuum in the pace-of-life syndrome, where short-lived, smaller organisms tend to produce a larger number of smaller offspring (Ricklefs 2000). Because slow pace of life in bird species are associated with lower BMR and cold-induced peak metabolic rates (Wiersma et al. 2007), birds with higher fecundity may have higher FMR, but we were unable to identify such an effect. Most species with low fecundity in our dataset were seabirds, and it is possible that the variation in FMR for terrestrial birds was relatively small. However, many other comparative studies of BMR (Speakman 2005, Bech et al. 2016) did not report any association between BMR and the pace-of-life syndrome, which is supported by our findings.

2.4.2 Field water flux

The scaling exponent for field water flux was 0.606, which was smaller than the value of 0.659 proposed by Tieleman and Williams (2002) but still within the 95% confidence interval. This difference may be due to our exclusion of certain albatrosses and storm-petrels that are strictly pelagic and are known to forage for an extended period of time without landing. These birds have high metabolic rates and water fluxes (e.g., Costa and Prince 1987). Our scaling exponent was also smaller than the allometric exponent of 0.68 for total evaporatory water loss at 25 ºC (Williams 1996). On the other hand, our exponent is very close to the value of 0.604 obtained from laboratory measurements of daily water fluxes (Degen et al. 1982), suggesting that body mass does not strongly interact with environmental factors such as water availability and exposure to outside temperature or humidity that may differ between laboratory and field conditions.

The 95% confidence interval for Pagel's λ did not include zero, which suggests that field water flux had residual phylogenetic covariance unexplained by body mass or environmental covariates. This result is in accordance with previous studies that found significant differences between conventional and phylogenetically informed analysis of field water flux (Tieleman and Williams 2000) and total evaporative water loss (Williams 1996) in birds. The total evaporative loss of marsupials also showed phylogenetic covariance to a smaller degree than predicted by a Brownian motion model (Withers et al. 2006).

Precipitation of the driest quarter had a positive correlation with field water flux as we predicted. This is in accordance with previous studies that suggested lower total evaporative water loss (Tieleman and Williams 1999) and field water flux (Tieleman and Williams 2000) in birds from arid climates. On the other hand, there was no significant correlation between field water flux and the mean temperature throughout the period of study. This suggests that, even though TEWL increases drastically at high temperatures, thermoregulatory demand for water does not have a strong effect in the field condition, where birds may be able to adjust their activity and microclimate to avoid extended periods of exposure to high temperatures (e.g., Carroll et al. 2015).

Increased salt intake mandates higher water flux to maintain osmotic balance. Seabirds had higher water flux than terrestrial birds. Although seabirds often engage in expensive foraging activities, the lack of significant differences between incubating and provisioning birds suggest that salt intake, rather than activity budget, may be connected to this difference. On the other hand, granivores did not have a statistically significant difference in field water flux from birds of other dietary habits. Many birds are known to drink from open water bodies when possible (e.g., Fisher et al. 1972, Beck et al. 1973), which may reduce the importance of preformed water in field conditions. Additionally, all seven species of granivores in this study occur in habitats of relatively low precipitation, and the effects of dry climate and of granivory may not have been identifiable in this case.

While non-breeding birds had significantly lower field water flux compared to breeding birds, the difference between incubating and provisioning birds was not statistically significant. Although seasonal changes in water flux had been previously documented (e.g., Webster and Weathers 2000), season was not a statistically significant predictor when inluded in models with body mass, suggesting that this difference in water flux cannot be explained by seasonal differences in temperature and precipitation through the breeding periods. While provisioning nestlings requires higher levels of activity compared to incubation, there was no significant differences between incubating and provisioning birds, suggesting that the change in water flux may be associated with exposure to less favourable microclimate conditions or physiological changes that accompany breeding.

2.4.3 Conclusion

As with laboratory measurements of metabolic rate and water flux, FMR and field water flux of birds were most strongly correlated with body mass. The correlation between ambient temperature and FMR and precipitation and field water flux suggest that environmental factors also have an influence. Seabirds with high levels of activity and sodium influx showed elevated levels of FMR and field water flux, and granivorous birds had lower FMR. Breeding birds had higher field water flux than non-breeding birds. From these relationships, we can see that behaviour and osmoregulation has significant effects on avian physiology in the field. Predictions based on field measurements instead of inference from birds under laboratory conditions will be greatly beneficial for a realistic evaluation of the physiological demands of birds.

Table 2.1. Models ranked by AICc for the null model, model including allometric relations only and the models including single additional predictors for FMR. “Mean temperature” and “mean monthly precipitation” refers to the mean temperature and mean monthly precipitation throughout the period of each study.

Predictor	Log-likelihood	AICc	ΔAICc
Log(body mass) + seabird	-27.29	60.83	0
Log(body mass) + diet	-26.63	63.87	3.04
Log(body mass) + mean temperature	-31.14	68.53	7.70
Log(body mass) + migration	-33.32	72.89	12.06
Log(body mass)	-34.59	73.30	12.47
Log(body mass) + mean monthly precipitation	-33.75	73.74	12.91
Log(body mass) + breeding status	-33.05	74.51	13.68
Log(body mass) + season of measurement	-34.59	75.41	14.58
Log(body mass) + annual clutch size	-34.59	75.42	14.59
(null)	-95.31	192.67	131.83

Table 2.2. Model-averaged coefficient estimates for FMR. All predictors were centred and normalised. “Mean temperature” and “mean monthly precipitation” refers to the mean temperature and mean monthly precipitation throughout the period of each study.

Predictor	Estimate	SE	p	cumulative AICc weight
Log(body mass)	0.885	0.048	<0.001	1.00
Mean temperature	-0.095	0.040	0.018	0.90
Seabird	0.275	0.113	0.015	0.90
Nectarivory	0.052	0.148	0.723	0.84
Omnivory	-0.126	0.078	0.108	0.84
Granivory	-0.368	0.126	0.004	0.84
Season (winter)	-0.121	0.105	0.249	0.43
Mean monthly precipitation	0.038	0.034	0.256	0.38
Annual clutch size	0.018	0.043	0.678	0.27
Migration	0.014	0.090	0.873	0.25
Phase (provisioning for young)	0.049	0.103	0.476	0.22
Phase (non-breeding)	-0.064	0.119	0.585	0.22

Table 2.3. Models ranked by AICc for the null model, model including allometric relations only and the models including single additional predictors for field water flux. "Mean temperature" refers to the mean temperature throughout the period of each study.

Predictor	Log-likelihood	AICc	ΔAICc
Log(body mass) + breeding status	-26.04	60.65	0
Log(body mass) + precipitation of the driest quarter	-27.23	60.80	0.15
Log(body mass) + seabird	-27.55	61.44	0.79
Log(body mass) + granivory	-28.97	64.28	3.62
Log(body mass)	-30.55	65.26	4.61
Log(body mass) + mean temperature	-29.89	66.12	5.47
(null)	-59.51	121.08	60.43

Table 2.4. Model-averaged coefficient estimates for water flux. All predictors were centred and normalised. "Mean temperature" refers to the mean temperature throughout the period of each study.

Predictor	Estimate	SE	p	cumulative AICc weight
Log(body mass)	0.787	0.064	<0.001	1.00
Precipitation of the driest quarter	0.106	0.043	0.014	0.85
Phase (non-breeding)	-0.339	0.142	0.017	0.77
Phase (provisioning for young)	-0.145	0.146	0.316	0.77
Seabird	0.443	0.205	0.030	0.75
Granivory	-0.325	0.176	0.065	0.62
Mean temperature	0.033	0.068	0.479	0.29

Figure 2.1. Relationship between significant predictors and FMR. Green data points are from seabirds and red data points are from terrestrial birds.

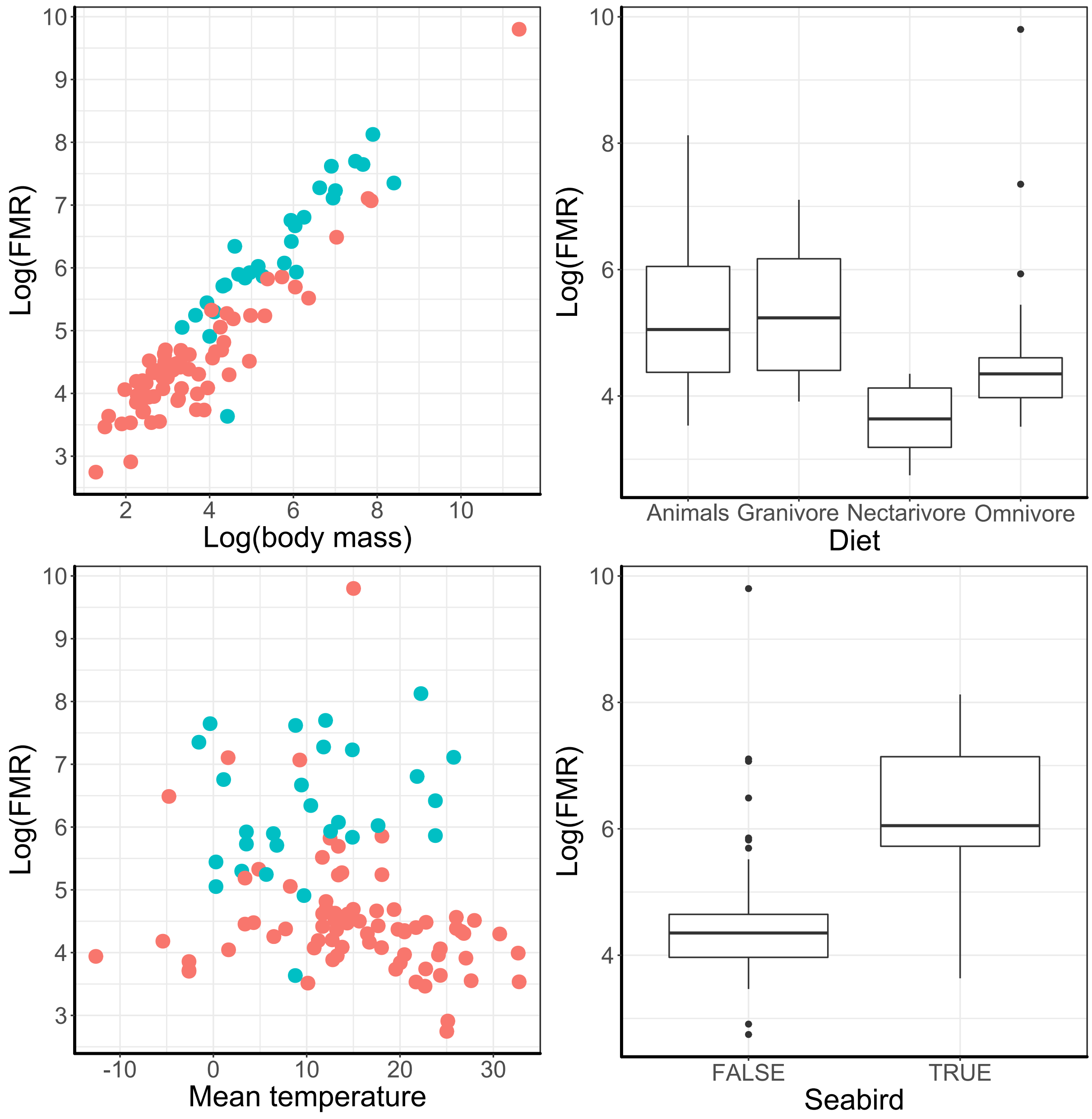


Figure 2.2. Comparison of coefficient values among predictors for FMR.

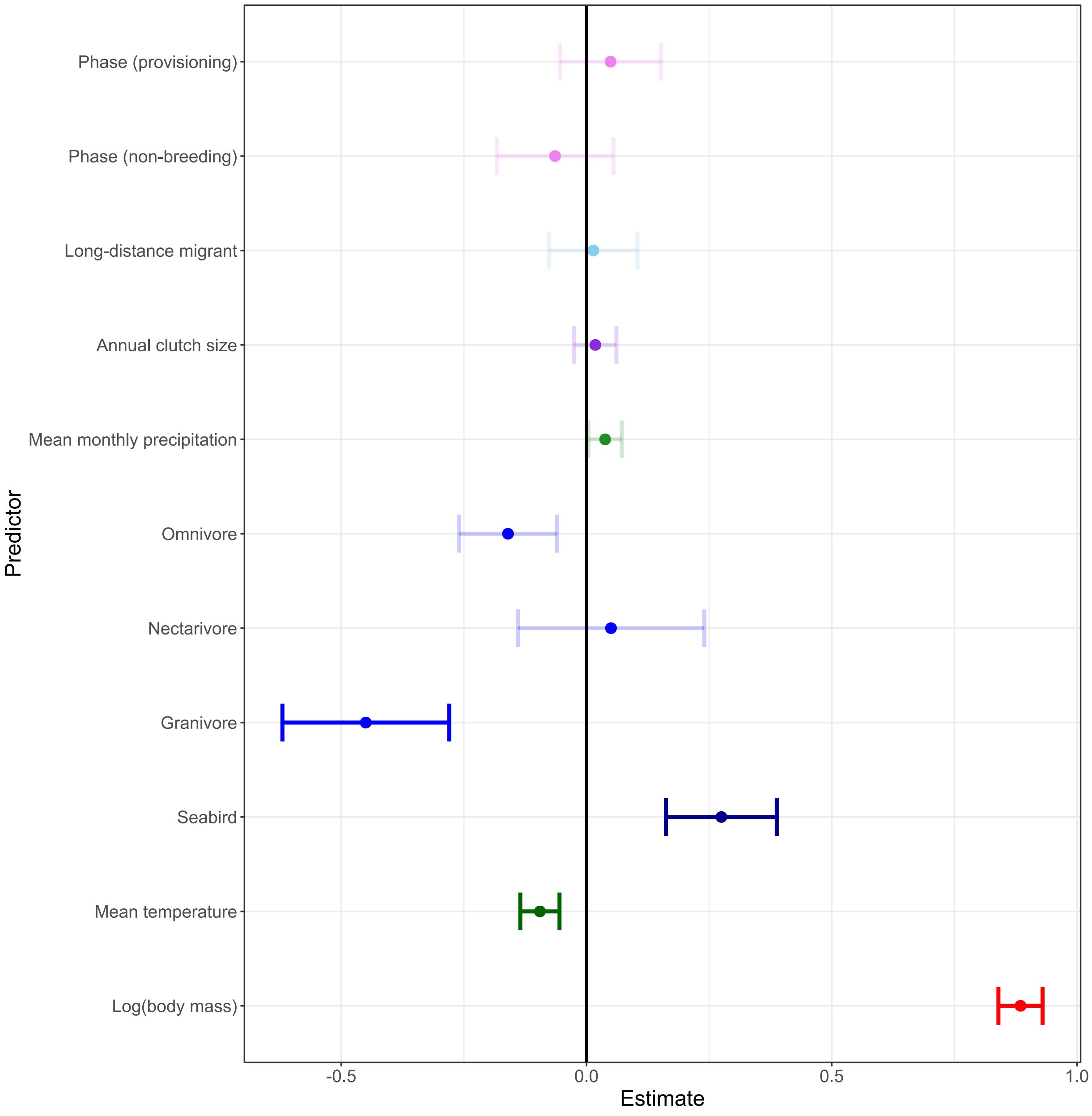


Figure 2.3. The relationship between significant predictors and field water flux. Green data points are from seabirds and red data points are from terrestrial birds. In the bottom right plot, “I” refers to incubating birds, “N” refers to non-breeding birds and “P” refers to birds provisioning for nestlings.

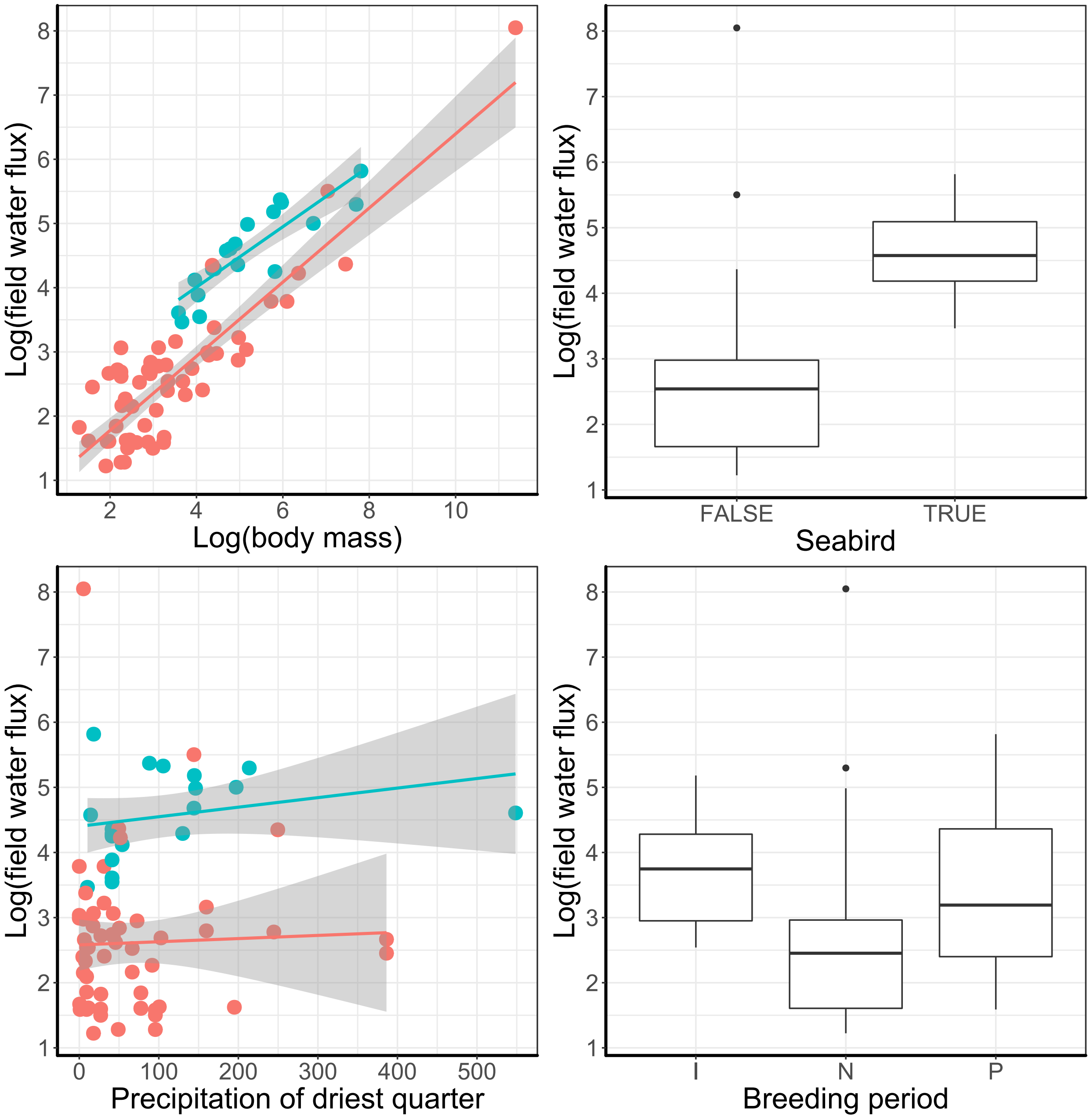


Figure 2.4. Comparison of coefficient values among predictors for field water flux.

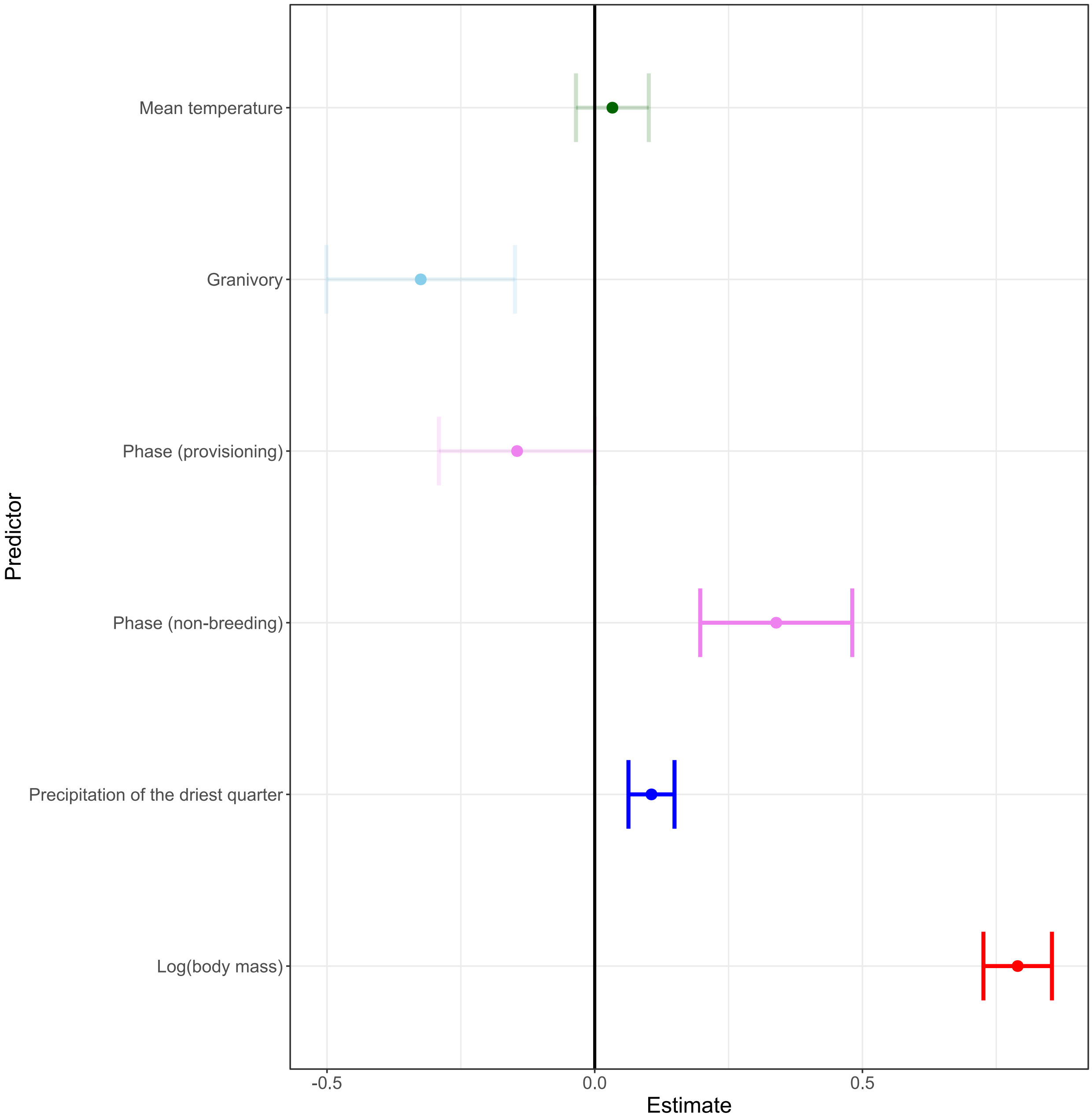


Figure 2.S1. Study locations for field metabolic rate.

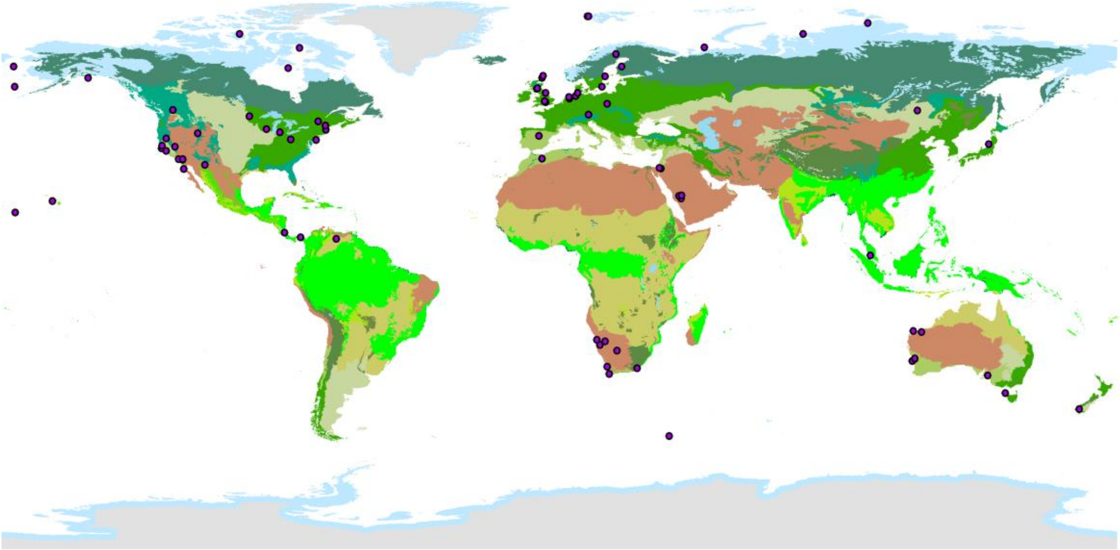
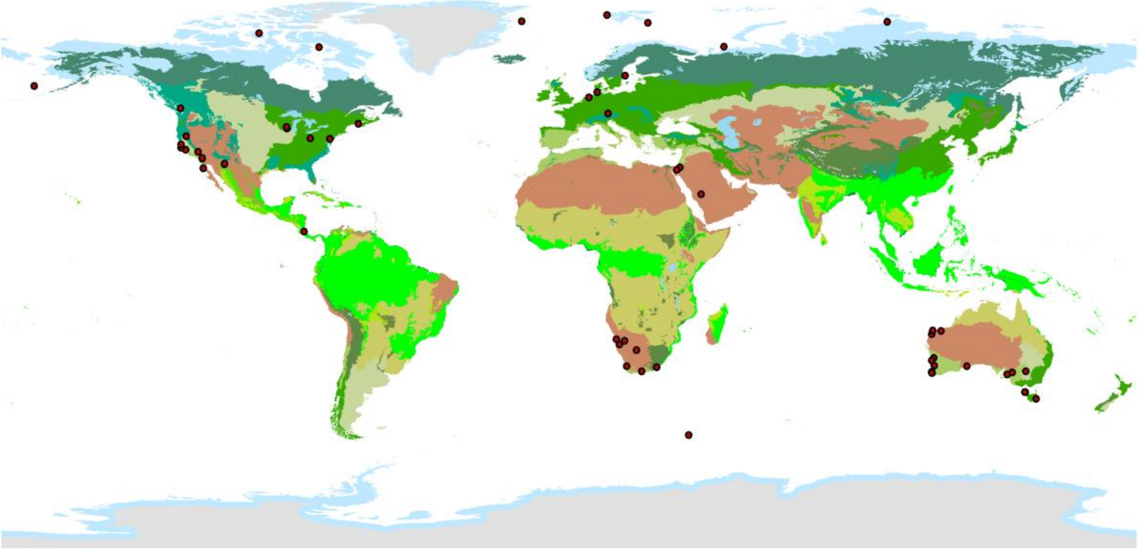


Figure 2.S2. Study locations for field water flux.



Chapter 3. The environmental determinants of evaporative water loss in birds at multiple temperatures

3.1 Introduction

Evaporation of water poses important challenges to terrestrial endotherms. The high metabolic rate of endotherms imposes heat load on the animal that must be dissipated into the environment (Speakman and Król 2010), often resulting in an elevated risk of desiccation by water evaporation. Dry heat transfer by convection and radiation is ineffective when atmospheric temperature is near the body temperature of an endotherm (Tomlinson 2016). When the ambient temperature is higher than the body temperature, an animal can no longer dissipate metabolic heat through convection (Smith et al. 2017). At this condition, heat dissipation through evaporative water loss is essential to maintain a relatively stable, non-lethal body temperature.

Under normothermic conditions, in which the contribution of evaporative water loss to the heat balance of an animal is minimal, it is beneficial to prevent the evaporation of water, especially when water is not readily available. Comparative studies of birds (Williams 1996) and mammals (Withers, Cooper, and Larcombe 2006) suggest that endotherms in arid habitats have lower evaporative water loss compared to those in more humid areas when they are not thermally stressed. Populations found in arid habitats often demonstrate lower evaporative water loss under thermoneutral conditions than those in non-arid habitats (e.g. MacMillen and Hinds 1998, Sabat et al. 2006). Furthermore, certain species of both mammals (Withers and Cooper 2014) and birds (Eto, Withers, and Cooper 2017) actively regulate water evaporation to prevent drastic increases in evaporative water loss at low relative humidity, highlighting the biological importance of the regulation of water evaporation.

An endotherm must balance the need to maintain a stable body temperature and prevent lethal dehydration. As most birds, unlike mammals, remain active throughout the daytime when ambient temperatures are relatively high, behavioural adaptation against exposure to hot air and to solar radiation is of limited utility. Physiological mechanisms such as countercurrent heat exchange in the nasal passage (Schmidt-Nielsen, Hainsworth, and Murrish 1970), heat dissipation through the bills (Hagan and Heath 1980, Greenberg et al. 2012) and hyperthermia (O'Connor, Brigham, and McKechnie 2017) enhance dry heat transfer and reduce evaporative water loss. From laboratory measurements of 28 avian species, Tieleman and Williams (1999) reported that bird species from arid habitats lost smaller quantities of water through evaporation at higher temperatures compared to those from a more mesic area. However, this finding was not supported by measurements of field water flux (Tieleman and Williams 2000). Some species in arid habitats (Tieleman, Williams, and Buschur 2002, Talbot et al. 2017) display high reliance on water evaporation. Intraspecific comparative studies also demonstrate conflicting results (Sabat, Gonzalez-Vejares, and Maldonado 2009, Noakes, Wolf, and McKechnie 2016), highlighting the importance of thermoregulatory challenges in physiological regulation of evaporative water loss when the ambient temperature is high.

A tradeoff between water conservation at low temperatures and efficient heat dissipation at high temperatures may occur if the total evaporative water loss of a bird is determined primarily by its anatomical features, or if the physiological factors governing evaporative water loss cannot be modified under short-term acclimation. On the other hand, birds are known to modulate total evaporative water loss (TEWL) in response to water deprivation (Lee and Schmidt-Nielsen 1971). Physiological mechanisms such as elevated respiratory rates (e.g., Crawford and Schmidt-Nielsen 1967) and gular fluttering (Bartholomew, Lasiewski, and

Crawford 1968) allow a bird to increase its respiratory evaporative water loss as a response to heat stress. Thus, it is possible that birds are capable of preserving water at lower temperatures and dissipating metabolic heat at higher temperatures with noticeable tradeoffs.

It is necessary to jointly address the effects of heat and water stress to understand the selective pressures driving interspecific variation in evaporative water loss. To do so, we must examine the effects of ambient temperature and humidity on the evaporative water loss under both normothermic and heat-stressed conditions. Williams (1996) and Tieleman and Williams (1999) reported reduced evaporative water loss for species in arid habitats, but the binary classification of arid versus mesic species does not adequately represent the full range of thermoregulatory challenges experienced by birds. Possible effects of high ambient temperatures or of low dietary water availability have not been addressed through comparative studies of evaporative water loss in birds. Additionally, the metabolic heat load experienced by an animal is determined by its metabolic rate, which varies significantly according to diurnal and seasonal cycles (e.g. Hinsley et al. 1993, Maddocks and Geiser 2000).

We evaluated the effect of temperature, aridity, and diet on the evaporative water loss of birds under normothermic condition and under heat stress, and on the slope of increase in evaporative water loss versus ambient temperature for temperatures above 35°C. We accounted for the phylogenetic relationship of birds (Jetz et al. 2012) and the effects of diurnal cycles of activity. By simultaneously examining these three responses, we attempted to identify the environmental correlates of evaporative water loss under increasing thermoregulatory challenge for birds. We predicted that water availability in the wild is likely to have a larger influence on TEWL at lower temperatures, while TEWL at higher temperatures will be associated with exposure to high ambient temperatures. We also predicted that measurements taken during the active phase will be higher than those taken during the resting phase, when the birds have higher resting metabolic rates and as a result generate a greater amount of metabolic heat.

3.2 Methods

3.2.1 Data collection

We compiled measurements on total evaporative water loss for 172 avian species (Figure 3.S1). To represent TEWL at normothermic conditions, measurements of TEWL at room temperature (25 °C) were used. Measurements at 40 °C, which is close to or higher than the upper critical temperatures of most birds (Khaliq et al. 2014), were used as TEWL for thermally stressed birds. Although respiratory evaporation is a major channel of evaporative water loss for birds, we did not include studies that measured respiratory evaporative water loss instead of total evaporative water loss. For species with measurements available at multiple temperatures, we transcribed the measured values of total evaporative water loss at 25 °C and 40 °C. When the values were not reported in the text, we used xyscan 4.3.0 (Ullrich 2017) to extract numerical values from figures. From these data, we also obtained the slope of increase in evaporative water loss above 35 °C.

Climatic information was obtained from the Worldclim dataset (Fick and Hijmans 2017), and species ranges were obtained from BirdLife International (Birdlife International and NatureServe 2015). We used the Zonal Statistics tool on ArcMap 10.2 (ESRI 2013) to average climatic information within 50km radius of the capture location. For 25 species in which the capture location was not included in the literature, and for 23 species whose measurements came from captive individuals, climate data was averaged across the entire range of the species or the subspecies. We followed the phylogeny provided by Jetz et al. (2012) for the phylogenetic relationship of all species in the dataset (Figure 3.S1). A total of 500 trees was sampled. As the use of consensus trees does not compromise the precision or accuracy of phylogenetically informed analysis (Rubolini et al. 2015), we averaged these 500 trees using the package phytools (Revell 2012) in R ver 3.4.4 (R Development Core Team 2018). Information on food habits of each species was obtained from McNab (2009) and from Handbook of the Birds of the World Alive (del Hoyo et al. 2018). We classified a species as granivorous if they were exclusively granivorous, or if a major proportion of the diet was granivorous.

Seasonal acclimatisation (e.g. Doucette and Geiser 2008, van de Ven, Mzilikazi, and McKechnie 2013) and phase of activity (e.g. Bartholomew and Trost 1970) influence the metabolic rate of an animal, which is a key determinant of endogenous heat load. We classified studies according to the daily time of measurement. If measurement was made within the bird's active phase, the determined resting metabolic rate would be higher than its basal metabolic rate. When the study had the objective to determine the basal metabolic rate of the animal, we assumed that the measurements were taken during the resting period of the circadian cycle unless indicated otherwise. Dates of measurement were available for 94 of the 172 species. Of these 94 species, 38 were either tropical or subtropical, where seasonal variation in thermal physiology is lower. Because of incomplete data, we did not include seasonal acclimatisation as a predictor.

3.2.2 Statistical analysis

We used body mass, seven bioclimatic variables (mean temperature, maximum temperature of the warmest month, minimum temperature of the coldest month, mean temperature of the driest quarter, annual precipitation, precipitation of the driest quarter and precipitation of the warmest quarter, obtained from the WorldClim dataset (Fick and Hijmans 2017)), activity phase and diet of the species (granivorous/not granivorous) as predictors. Response variables included total evaporative water loss at 25 ºC (n=171) and 40 (n=98) ºC and the slope of measured values of evaporative water loss above 35ºC (n=84). While measurements from 26 species reported inflection points for the evaporative water loss curves, the segmented linear regression method (Muggeo 2003) used to obtain these values produced extremely wide confidence intervals, and in some cases did not identify a breakpoint. The values obtained by this method were also inconsistent with some reported inflection point values. Accordingly, we did not use these reported values.

Due to high collinearity within the bioclimatic variables we initially examined (Table 3.1), we selected the climatic variables that were the most relevant to the hypothesis at hand. For evaporative water loss at 25ºC we used the precipitation and the temperature of the driest quarter, where water limitations are expected to be the most influential. For the evaporative water losses at higher temperatures, where thermal stress has a larger role, we chose the maximum temperature and the precipitation of the warmest quarter. Additionally, we included two-way interaction terms between temperature and activity phase, and between precipitation and granivory. To make the coefficients comparable, all continuous predictors, including body mass, were centred and normalised prior to the analysis.

Evaporative water loss is known to be allometrically related to body mass (Williams 1996). We therefore log-transformed body mass and all evaporative water losses to linearise the relationship. To account for phylogenetic non-independence, we analysed the dataset by PGLS with the package caper (Orme et al. 2013) in R 3.4.4 (R Core Development Team 2018) with the Brownian motion model and Pagel's lambda set as the maximum-likelihood value. For all three responses, we first compared the model including only the body mass to those with single environmental and ecological variable added to the model. Then, we constructed a full model including temperature, precipitation, activity phase, granivory and body mass with two-way interactions between precipitation and granivory and temperature and activity phase. Because all models included two-way interactions, conditional instead of full average coefficient estimates are reported. These estimates were compared with the best model by AICc and final model from a backward stepwise selection by AICc. AICc and AICc weights were calculated by the Package MuMIn (Barton 2018) in R 3.4.4 (R Core Development Team 2018).

3.3. Results

3.3.1 Evaporative water loss at 25 ºC

Comparison between models with body mass and a single additional predictor (Table 3.2) suggested that body mass and activity phase were major determinants of total evaporative water loss at 25ºC, with only the addition of activity phase improving the model. Model-averaged estimates with the full model including annual mean temperature, activity phase, precipitation of the driest quarter, granivory, activity phase and body mass, along with a two-way interaction between the annual mean temperature and activity phase and the precipitation of driest quarter and granivory and all nested models revealed effects of body mass, activity phase and the interaction between precipitation of the driest quarter and granivory (Figure 3.1, Table 3.3). Body mass, acctivity phase and the interaction between precipitation and granivory were the most important predictors based on cumulative AICc weights. This was generally in agreement with the best model selected both by AICc and by backward stepwise selection, which included significant effects of body mass, actrivity phase, precipitation of the driest quarter, and the two-way interaction between precipitation of the driest quarter and granivory. The maximum likelihood estimate for Pagel's λ for this model was 0.714 with 95% confidence interval of (0.322, 0.930), indicating a relatively high phylogenetic correlation in residuals.

3.3.2 Evaporative water loss at 40 ºC

The maximum temperature of the hottest month and activity phase were the only two predictors that improved model performance when added to the base model with body mass to describe variation in evaporative water loss at 40ºC (Table 3.4). Full model comparison with the maximum temperature of the hottest month, precipitation of the warmest quarter, granivory, activity phase and body mass, along with two-way interactions between activity phase and maximum temperature of the hottest month and granivory and precipitation of the warmest quarter, suggested significant effects of body mass, activity phase and a two-way interaction between the maximum temperature of the hottest month and activity phase (Figure 3.2, Table 3.5). This was in agreement with the best model by AICc and backward stepwise model selection. Pagel's λ for the best model by AICc had a maximum likelihood estimate of 0.374 with a 95% confidence interval of (0, 0.753), which was lower than the maximum likelihood estimate for λ in the best model for TEWL at 25 ºC.

3.3.3 Slope of TEWL above 35 ºC

For the slope of TEWL, activity phase and maximum temperature of the hottest month were the only predictors that improved model performance when added to a model only containing body mass (Table 3.6). There were significant effects of the maximum temperature of the hottest month, activity phase, body mass, granivory and a two-way interaction between the maximum temperature and activity phase (Figure 3.3, Table 3.7). This result was in agreement with the final model by backward selection and the best model by AICc. Pagel's λ from this model had a maximum likelihood estimate of 0.813, with the 95% confidence interval of (0.351, 1), which was higher than the estimate for TEWL at 25ºC but overlapped considerably.

3.4 Discussion

Body mass was the most important predictor for evaporative water loss under all three conditions. The estimated allometric exponent for TEWL at 25°C was 0.65, close to Williams (1996)'s exponent of 0.678 but smaller than the PGLS allometric exponent of 0.73 for marsupials reported by Withers, Cooper and Larcombe (2006). For TEWL at 40°C the estimate was 0.71, which was close to the exponent at 25°C but much higher than the exponent of 0.56 at 45°C reported by Tieleman and Williams (1999). Interestingly, this value was very similar to our estimate for the allometric exponent of the slope above 35°C, likely because the majority of the slope estimates were obtained from measurements for high temperatures ranging up to 50 °C. All analysis had point estimates of Pagel's λ greater than zero, suggesting that the usage of phylogenetic comparative methods was justified. However, the 95% confidence intervals were extremely wide for all three variables, with the confidence intervals spanning the entirety of the range of possible Pagel's λ values.

Our analysis suggests that trends in TEWL at 25 and 40°C, along with the slope of TEWL above 35°C, are associated with different environmental and biological covariates. At the normothermic temperature of 25°C, the best model included a small negative effect of precipitation of the driest quarter on evaporative water loss (Figure 3.1), although this did not agree with the model-averaged coefficient estimates (Table 3.3). As indicated in some interspecific (Williams 1996, Williams and Tieleman 2002) and intraspecific (Sabat et al. 2006) comparative studies, it is possible that this effect connects lower water availability with conservation of water through a lower TEWL. However, contrary to our predictions, there was a significant positive interaction between precipitation and granivory. While the diet of granivorous birds contains a large amount of dry matter, these birds drink surface water when it is available (e.g., Smyth and Coulombe 1971, Fisher, Lindgren, and Dawson 1972, Lee, Wright, and Barnard 2017). As the metabolic trials were generally undertaken without exposing the birds to water stress, it is possible that the drinking habits of granivores allowed them greater water availability when water was presented *ad libitum*. On the other hand, because birds within a metabolic chamber are not presented with drinking water throughout the trial (Lighton and Halsey 2011), granivores will not be able to offset the large amounts of TEWL at higher temperatures.

TEWL at 40°C (Figure 3.2) and the slope of TEWL above 35°C (Figure 3.3) were not associated with precipitation, although there was a negative effect of granivory on the slope of TEWL above 35°C. This result was contrary to a previous comparative study, which reported that desert birds had lower TEWL at both 25 °C and 45°C (Tieleman and Williams 1999). It is possible that water conservation has a smaller influence at higher temperatures. Contrary to our predictions, birds in the resting phase showed a small negative relationship between maximum environmental temperature and TEWL at high temperatures. On the other hand, this effect was not seen for active birds at 40°C. Additionally, the relationship between maximum temperature and the slope of TEWL above 35°C was positive for birds in the active phase. The majority of slopes were obtained from measurements that extended to extreme temperatures up to and above 50°C. At such a condition, environmental temperature is higher than the body temperature of a bird, necessitating water evaporation as a mechanism of heat dissipation (McKechnie et al. 2016).

Activity phase was a significant predictor for all response variables. Birds in their resting phase generally demonstrated lower TEWL compared to birds at the active phase. Activity has been noted as a possible confounding factor that may affect the accuracy of the estimates of basal metabolic rates (McKechnie and Wolf 2004), but its effect on TEWL estimates has not been previously addressed. Furthermore, at higher temperatures, birds in resting and active phase differed in their relationship between ambient temperature and TEWL, with negative correlation between ambient temperature and TEWL for resting birds and positive correlation between these two variables for active birds. This effect of activity on thermoregulation had not been addressed in detail, although some studies suggest that birds in the active phase tolerate higher temperatures than in the resting phase (Hudson and Kimzey 1966, Hinsley et al. 1993). It is possible that increase in heat dissipation through evaporative water loss functions as a mechanism for birds in hotter regions to tolerate higher temperatures. Although it is unrealistic to attempt to simultaneously minimise the effect of captivity while conducting all trials during the resting phase, studies comparing TEWL at higher temperatures for active and resting birds will help elucidate the potential mechanisms behind this effect.

Overall, the effects of allometry and activity phase were generally larger than that of environmental covariates. There is a possibility that sampling bias at least partially contributed to this finding. Almost half of the 172 avian species covered in this study were found in arid or semiarid habitats, and the capture locations of these species (Figure 3.S2) were distributed unevenly across the globe. The arid and semiarid species were captured mostly in subtropical deserts. There is relative paucity of measurements taken from humid tropical birds, boreal birds, or birds from relatively cold arid habitats. Thus, this dataset may not be adequate to represent the entire range of thermal environments faced by birds, and future experimental studies would benefit greatly from sampling from those areas and habitats that have been overlooked. Additionally, although humidity alters both the mechanism and amount of evaporative water loss in birds (Gerson et al. 2014), most studies did not record relative humidity in the metabolic chamber throughout the experiment. While seasonal acclimation (e.g., Cooper and Gessaman 2004) and plumage characteristics (e.g., Ellis 1980) influence heat load by metabolism and solar radiation as well as the capacity for heat dissipation, many studies did not indicate the dates of capture and of the experiment, making it impossible to address these effects.

Table 3.1. Correlation coefficients for climatic predictors of the dataset. T_{mean}=annual mean temperature, T_{max}=maximum temperature of the hottest month, T_{min}=minimum temperature of the coldest month, T_{dry}=mean temperature of the driest quarter, P_{ann}=annual precipitation, P_{dry}=precipitation of driest quarter, P_{warm}=precipitation of warmest quarter. Values in bold face are significant after Bonferroni correction for multiple comparison.

	T_{mean}	T_{max}	T_{min}	T_{dry}	P_{ann}	P_{dry}	P_{warm}
T_{mean}	1						
T_{max}	**0.876**	1					
T_{min}	**0.938**	**0.658**	1				
T_{dry}	**0.910**	**0.749**	**0.901**	1			
P_{ann}	0.178	-0.125	**0.367**	0.110	1		
P_{dry}	0.034	**-0.217**	0.207	0.007	**0.906**	1	
P_{warm}	0.169	-0.059	0.304	0.008	**0.934**	**0.837**	1

Table 3.2. Models ranked by AICc for the null model, model including allometric relations only and the models including single additional covariates for TEWL at 25°C. AICc value for the best model was 539.99.

Terms in model	df	Log-likelihood	ΔAICc
Log(mass) + activity phase	3	-266.92	0
Log(mass)	2	-270.00	4.09
Log(mass) + precipitation of driest quarter	2	-269.37	4.90
Log(mass) + granivory	3	-269.88	5.92
Log(mass) + annual mean temperature	3	-270.00	6.16
(null)	1	-288.90	39.85

Table 3.3. Model-averaged coefficient estimates for TEWL at 25°C for 171 avian species. P_{dry}=precipitation of driest quarter.

Covariates	Estimate	SE	Cumulative AICc wt
Log(mass)	1.148	0.159	1
Precipitation of the driest quarter	-0.227	0.145	0.65
Granivory	-0.213	0.273	0.63
Activity phase ρ	-0.508	0.195	0.91
P_{dry}*granivory	0.461	0.177	0.49

Table 3.4. Models ranked by AICc for the null model, model including allometric relations only and the models including single addtiional covariates for TEWL at 40ºC. AICc value for the best model was 87.06.

Terms in model	df	Log-likelihood	ΔAICc
Log(mass) + maximum temperature of hottest month	3	-40.4	0
Log(mass) + activity phase	3	-45.65	10.49
Log(mass)	2	-47.33	11.72
Log(mass) + granivory	3	-46.35	11.90
Log(mass) + precipitation of warmest quarter	3	-46.78	12.76
(null)	1	-117.29	149.56

Table 3.5. Model-averaged coefficient estimates for TEWL at 40ºC for 98 avian species. T_{max} = maximum temperature of the hottest month.

Covariate	Estimate	SE	Cumulative AICc wt
Log(mass)	1.050	0.0488	1
T_{max}	-0.078	0.0656	1
Activity phase ρ	-0.174	0.0749	0.96
T_{max} * phase	-0.161	0.0731	0.77

Table 3.6. Models ranked by AICc for the null models, model including allometric relations only and the models including single addtiional covariates for the slope of TEWL above 35ºC. AICc value for the best model was 109.31.

Terms in model	df	Log-likelihood	ΔAICc
Log(mass) + phase	3	-51.49	0
Log(mass) + maximum temperature of the hottest month	3	-51.79	0.59
Log(mass)	2	-53.35	1.56
Log(mass) + granivory	3	-52.80	2.60
Log(mass) + precipitation of the warmest quarter	3	-53.08	3.18
(null)	1	-83.68	60.10

Table 3.7. Coefficient values for the best model for the slope of TEWL above 35ºC for 84 avian species. T_{max} = maximum temperature of the hottest month.

Covariate	Estimate	SE	Cumulative AICc wt
Log(mass)	0.730	0.075	1
T_{max}	0.335	0.086	1
Activity phase ρ	-0.209	0.102	1
Granivory	-0.341	0.146	0.85
T_{max} * phase	-0.364	0.115	0.99

Figure 3.1. The relationship between significant predictors and TEWL at 25ºC. In figure 3.1B, green circles are measurements from granivorous birds while red circles are measurements from non-granivorous birds.

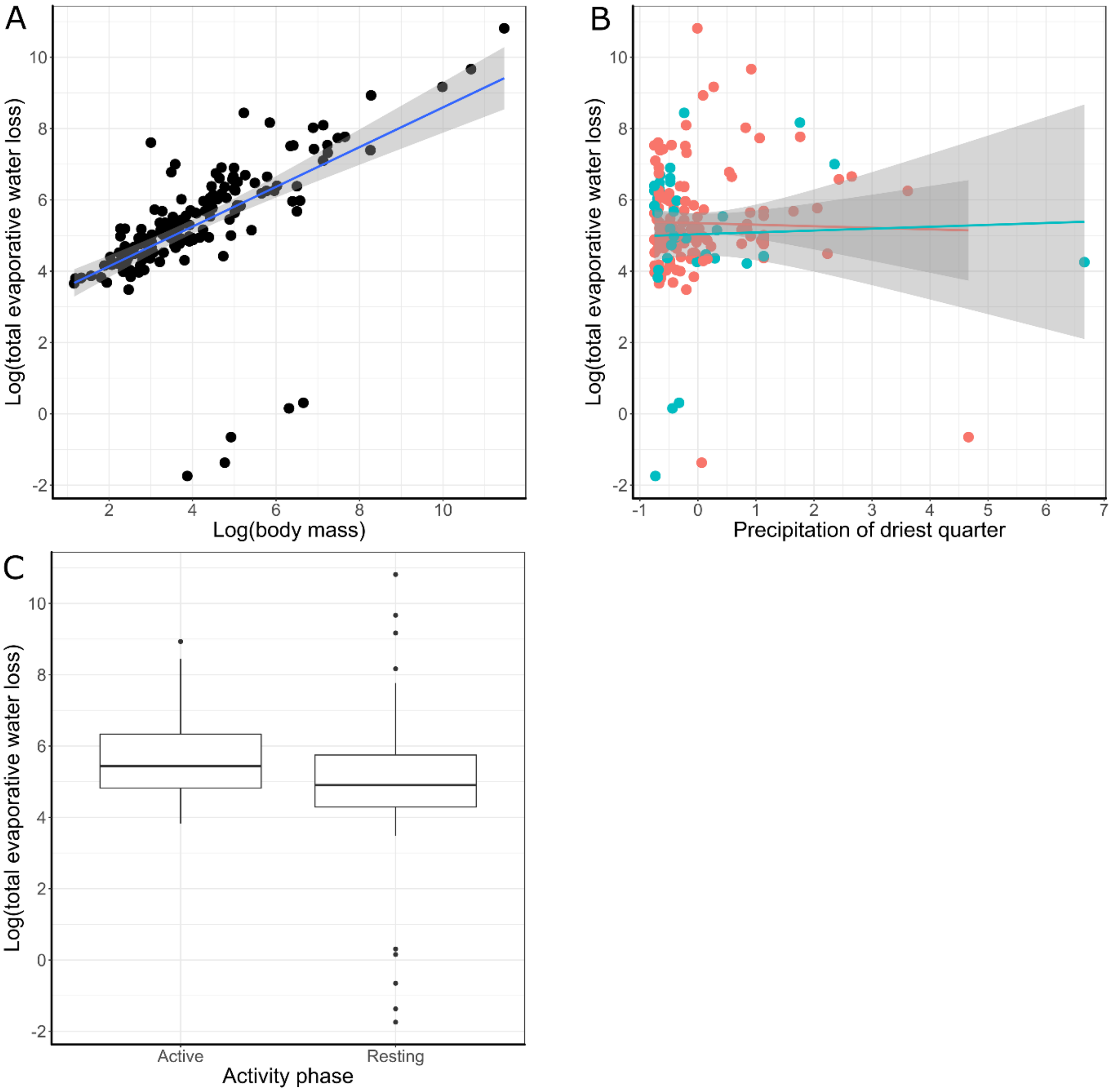


Figure 3.2. The relationship between significant predictors and TEWL at 40ºC. In Figure 3.2B, green circles are measurements from the resting phase while red circles are measurements from the active phase.

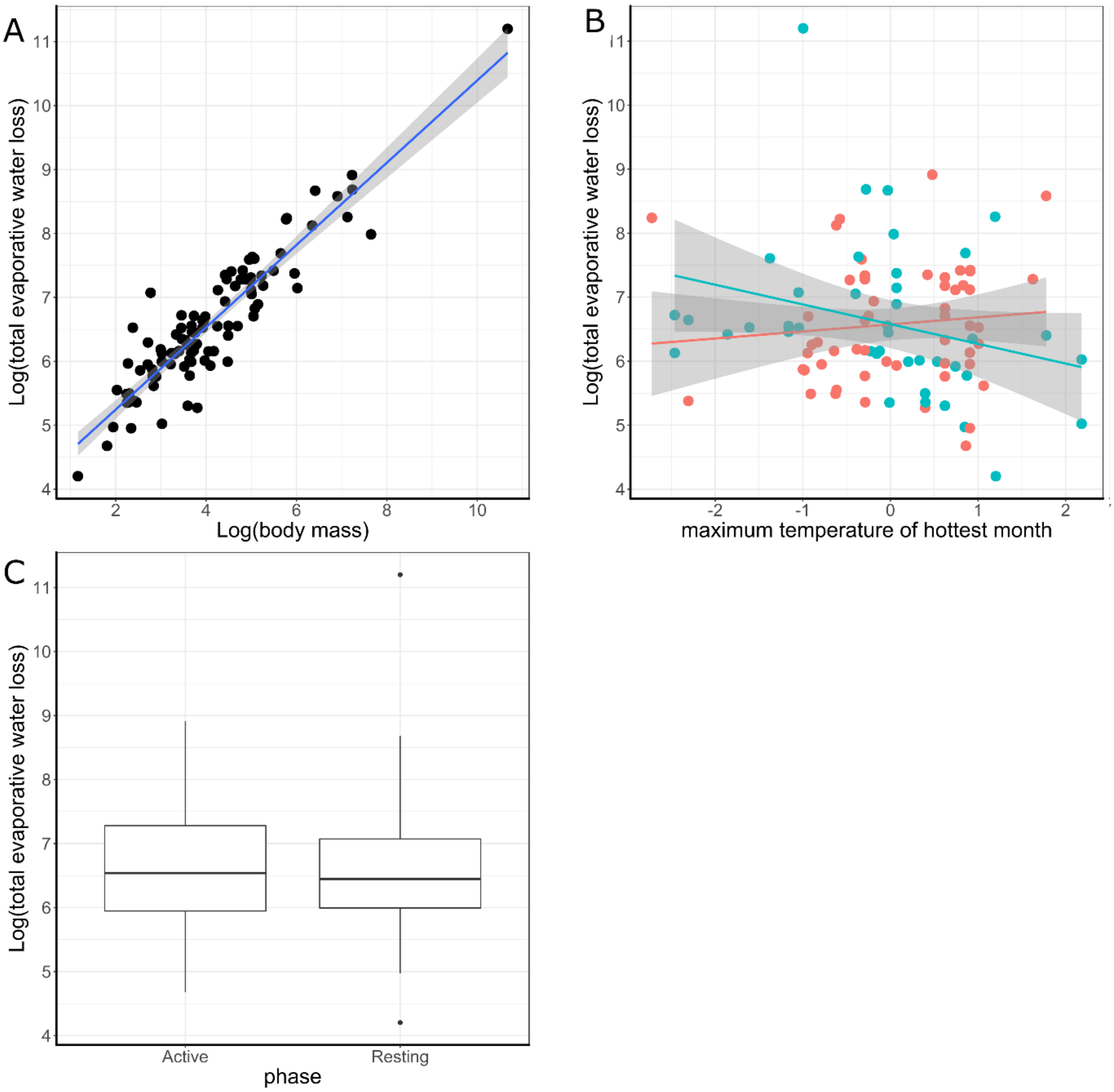


Figure 3.3. The relationship between significant predictors and the slope of TEWL above 35ºC. In Figure 3.3B, green circles are measurements from the resting phase while red circles are measurements from the active phase.

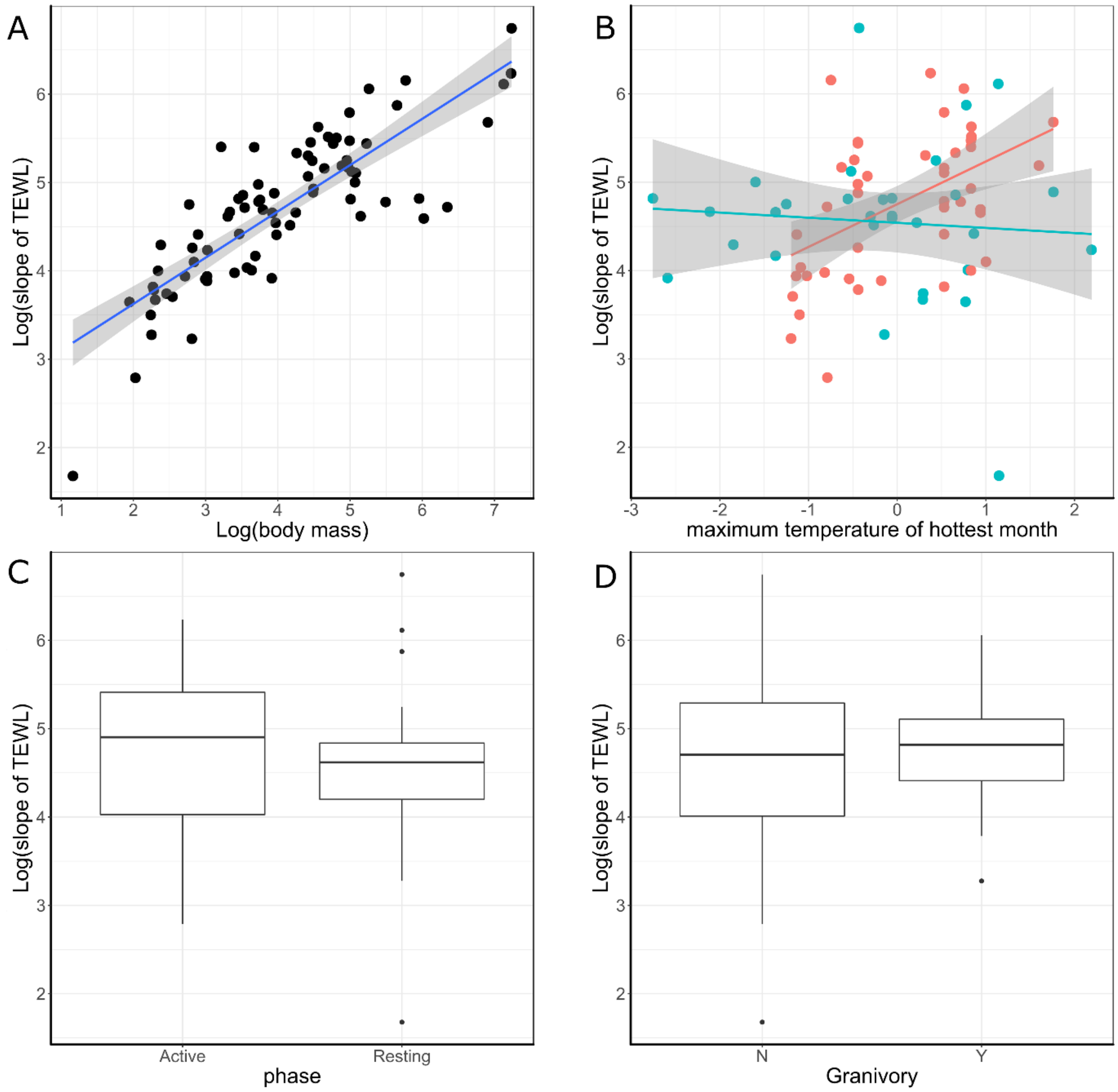


Figure 3.S1. The phylogenetic tree of all species included in the analysis.

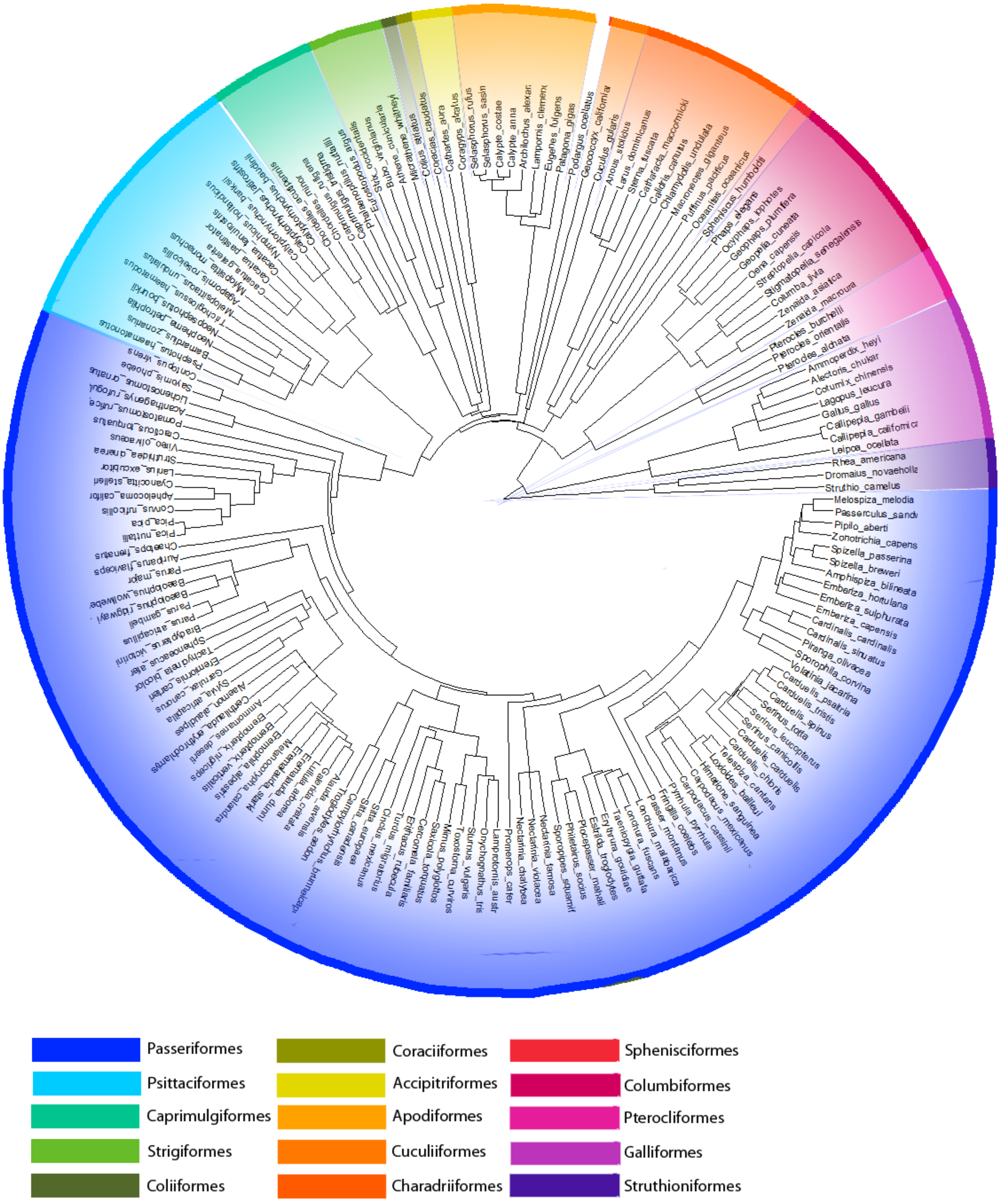
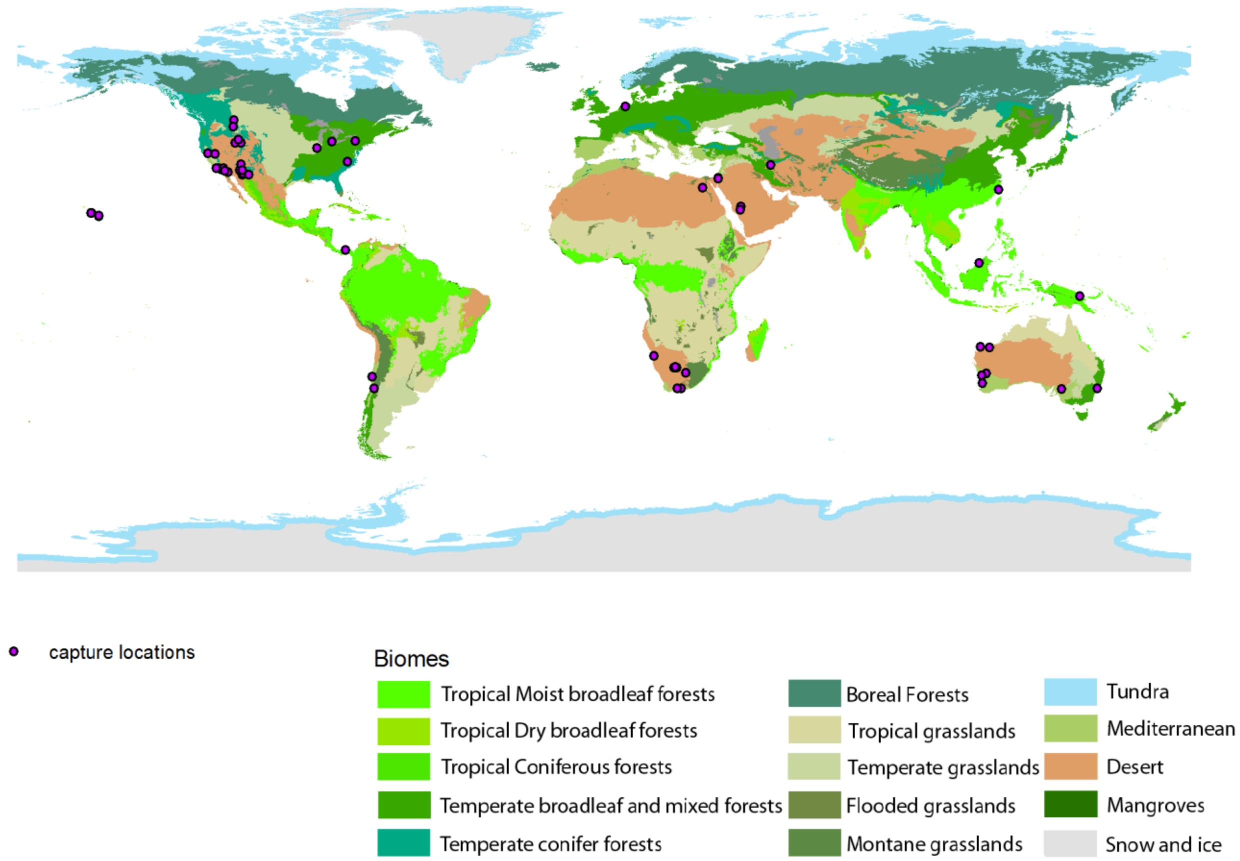


Figure 3.S2. Capture locations for avian species used in this analysis. Biomes are classified according to Olson (2001).



Chapter 4. Interspecific variation of upper critical temperatures in birds and the effect of data quality

4.1 Introduction

Because temperature affects all biochemical reactions, the metabolism of an animal depends on the ambient temperatures to which the animal is exposed. The body temperature (T_b) of an ectothermic animal is close, or equal, to the ambient temperature (T_a). As a result, their metabolic rate can be described by a thermal performance curve (Schulte 2015) that responds rapidly to T_a as well as to their activity levels (Huey and Stevenson 1979). Endotherms, on the other hand, maintain a relatively stable T_b that is usually higher than ambient temperature. Their metabolic rate is lowest in the absence of metabolic heat production above that required for tissue maintenance and of active heat dissipation to prevent hyperthermia under high ambient temperatures (Rezende and Bacigalupe 2015). This temperature range is called the thermoneutral zone (TNZ), the T_a in which an endotherm does not expend additional energy for thermoregulation.

The Scholander-Irving model (Scholander et al. 1950) predicts that an endotherm will generate metabolic heat to maintain a stable body temperature at temperatures lower than the TNZ. This is a well-supported mechanism of increase in metabolic rates below the TNZ. Above the upper limit of the TNZ, or the upper critical temperature (UCT), however, the mechanism of the increase in metabolism and its effect in thermoregulation is less straightforward. For endotherms that display hyperthermia above the TNZ, the elevated body temperature increases metabolic rates (Tomlinson 2016) and contributes to increased heat dissipation through increase in thermal conductance (Tieleman and Williams 1999). Increase in evaporative water loss, which is a major mechanism of heat dissipation for endotherms, also contributes to the increased metabolic rate (Rezende and Bacigalupe 2015). Unlike at ambient temperatures below the LCT where energetic costs of metabolic heat production is the primary limiting factor, ambient temperature and humidity (Gerson et al. 2014), water availability (McKechnie and Wolf 2010) and the effect of increased metabolic heat limit the efficiency of heat dissipation at high temperatures. When water is not readily available, or when ambient humidity and temperature renders evaporative heat loss ineffective, temperatures above the TNZ can severely limit the activity of an endotherm (du Plessis et al. 2012).

Despite the potential importance of upper critical temperatures as a determinant of the abiotic climatic effects on a species, UCT has not been extensively studied. Araujo et al. (2013) examined the thermal tolerance limits of plants, ectotherms and endotherms and concluded that the upper thermal tolerance limits are less variable than lower thermal tolerance limits across all taxa. They also suggested that critical limits to heat are largely uncorrelated with environmental temperature metrics and that there are hard, biochemical constraints that prevent adaptation to higher temperatures. In their analysis of TNZ breadth in endotherms, Khaliq et al. (2014) concluded that UCT is less variable than LCT, and in a subsequent study (Khaliq et al. 2015) suggested that UCT had a greater dependence on environmental conditions in temperate than in tropical climates, lending support to the possibility that hard physiological limits constrain adaptation to temperatures above a threshold.

The detrimental effects of a high body temperature has a well-documented molecular basis (e.g. Velichko et al. 2013), making it likely that UCT will be limited by the temperature at which heat dissipation is no longer effective. Whille environmental correlates can explain some of the variance in the UCT of endotherms (Khaliq et al. 2015), the factors that determine UCT below the physical limit of heat dissipation have not been extensively studied. The importance of water evaporation as a thermoregulatory mechanism suggests that water availability as well as ambient temperature may influence the ability to tolerate high temperatures without elevated metabolic rates (McKechnie and Wolf 2010). While migratory species may be able to avoid temperature extremes, their capability to migrate requires the ability to produce metabolically expensive tissue. There has not been an explicit evaluation of the effect of migration on the thermal tolerance of endotherms, or whether the presence of hard physiological limits influences the lower and upper bounds of interspecific variation in UCT. If these limits do not have a strong influence on the lower bound of UCT, temperate and boreal endotherms as well as tropical species may experience physiological thermal stress.

Data quality further clouds the relationship between UCT in birds and potential covariates (Wolf et al. 2017). UCT is estimated by measuring the changes in metabolic rates as temperature is increased, and the reliability of this measurement can vary widely. The difficulty of achieving precise temperature increments in the lab resulted in some studies with measurement intervals of ≥ 5ºC (e.g., Mann 1983, Merola-Zwartjes 1998). Some researchers halted measurement when they decided that the UCT was reached, making it impossible to estimate UCT without bias (e.g., McNab 2003). Moreover, the statistical methods used to estimate UCT (Muggeo 2003, Toms and Lesperance 2003) are not robust against these issues. Many studies simply report mean values and standard deviations of metabolic rates at each temperature instead of presenting measured metabolic rates for each individual (e.g., Wilson, Brown, and Downs 2011, Xia et al. 2013, Gavrilov 2015), making it impossible to estimate confidence intervals for UCT by bootstrapping. As a result, UCT estimates are less precise and less accurate than those of other thermal physiological variables. Hof et al. (2017) claimed that screening by data quality as suggested by Wolf et al. (2017) did not result in significant changes to their predictions. However, they examined the breadth of TNZ, which is more heavily influenced by LCT than UCT (Khaliq et al. 2014). The effect of data quality on the estimation of interspecific variation on UCT remains to be addressed. Additionally, even though birds demonstrate elevated metabolic rates through their active phase of the circadian cycle (McKechnie and Wolf 2004b), the effect of activity phase on UCT has not been examined.

In this study we address the effects of ambient temperature, water availability and migratory habit on the interspecific variation of UCT in birds. We incorporated phylogenetic relationship (Jetz et al. 2012), circadian cycles of activity, and classification by data quality as suggested by Wolf et al. (2017). We also examined whether there were greater influences of ambient temperature on species with lower UCT. We predicted that high UCT will be positively correlated with high ambient temperature, and that migratory species and species with diurnal measurements will display lower UCT compared to sedentary species and the birds sampled at night. Finally, we predicted that the inclusion of lower quality data will result in lower precision and a reduced estimate of phylogenetic signal as due to a greater magnitude of error, and in lower coefficient values for UCT due to UCT undersettimation by absence of measurements at higher temperatures.

4.2 Methods

4.2.1 Data collection

We compiled estimates of the upper critical temperatures of 210 avian species (Figure 4.S1). When UCT estimates were reported by the authors, we recorded those reported values as the UCT of the species. If UCT was not given but increase in metabolic rate above that at TNZ was reported, we estimated UCT by visual inspection of the data, because segmented linear regression often had unreasonably large confidence intervals and did not match visual inspection. Some studies included measurements of metabolic rate above 35ºC but without a clear UCT. For these studies, we recorded the highest measured temperature and whether it was above 35ºC or 40ºC. For all of these studies, birds were resting and postabsorptive without additional food or water provided during measurement.

Data quality was categorised using a modificcation of the scheme suggested by Wolf et al. (2017): (1) sufficient data - measurements of metabolic rate for two or more distinct temperatures above UCT with an interval of at least 2ºC between temperatures; (2) insufficient data - metabolic rates reported above the UCT for a single temperature or at temperatures with intervals less than 2ºC; (3) UCT reported but without evidence – studies that reported UCT had been reached but without graphical evidence; and (4) UCT not reached – studies that did not report UCT and did not contain visual evidence of UCT having been reached. Among the 210 species, 91 were in category 1, 61 in category 2, 28 in category 3 and 30 in category 4.

For phylogenetic relationship, we sampled 500 phylogenetic trees from the dataset provided by Jetz et al. (2012). These were averaged using the package phytools (Revell 2012) in R ver 3.4.4 (R Development Core Team 2018).

We obtained information on modern climate from the Worldclim dataset (Fick and Hijmans 2017). The coordinates of capture locations were available for 120 species. Measurements on 90 species had been taken from either captive individuals or unspecified locations. For these species, we obtained species range information from BirdLife International (Birdlife International and NatureServe 2015). We used the Zonal Statistics tool on ArcMap 10.2 (ESRI 2013) to average climatic information within 50km radius of the capture location, or within the range of the species, the subspecies or the population. Climatic variables included annual mean temperature, maximum temperature of the hottest month, temperature seasonality as defined by standard deviation, mean temperature of the warmest month, annual temperature range, annual precipitation, and precipitation of the warmest quarter (Fick and Hijmans 2017).

Three categorical predictors of UCT were examined: food habit, migratory status and time of measurement in the circadian cycle. Data on food habit and migratory status of each species was obtained from Handbook of the Birds of the World Alive (del Hoyo et al. 2018). We classified a species as granivorous if a major proportion of its diet was seeds. For migratory habits, we classified the bird into two categories: migrants and residents, with migrants having distinct breeding and wintering ranges. Studies were also classified based on whether measurements of metabolic rates were taken during the resting phase or during the active phase. When the study reported basal metabolic rates without referring to active-phase measurements, we assumed that the study took place during the resting phase.

4.2.2 Statistical analysis

Due to high collinearity among some climatic variables (Table 4.1), we only included maximum temperature of the hottest month, temperature seasonality, and precipitation of the warmest quarter in the model set. Biological predictors included were migratory status, granivory, log-transformed body mass, and whether UCT was measured during the resting or active phase of the bird. As the response, we used upper critical temperatures compiled from the literature. Two-way interactions between maximum temperature of the warmest month and migration, temperature seasonality and migration, and granivory and precipitation of the warmest quarter were included in the model set.

For 180 of the 210 species, UCT was recorded as continuous response analysed by PGLS with the package caper (Orme et al. 2013) in R 3.4.4 (R Core Development Team 2018) with Pagel's λ set as the maximum-likelihood value. Using AICc values computed by the package MuMIn (Barton 2018) in R 3.4.4. (R Core Development Team 2018), we compared single-predictor models with the null model. We next constructed a full model that included all main effects and the specific two-way interactions. We calculated AICc weights and model-averaged parameter estimates with the package MuMIn (Barton 2018). Because the model included two-way interactions, we used the conditional averages. These estimates were compared with the best model by AICc and with the final model from backward stepwise selection using AICc. We also examined the residuals from the model-averaged estimate against UCT for signs of non-independence to determine whether negative residuals were more common at higher UCT.

We analysed the binary responses of minimum UCT being above 35 (n=210) and above 40ºC (n=200) with phylogenetic logistic regression (Ives and Garland 2010). We constructed a full model identical to the one used in the continuous response and compared this model with all nested models. This method performs logistic regression on a phylogenetically correlated response with the assumption that the expected value of the binary dependent variable is phylogenetically correlated. We conducted this analysis by the package phylolm (Ho, Si, and Ané 2014) in R 3.4.4 with 300 bootstrap samples for each model. We compared the models by AIC and Akaike weights due to the lack of a definition for AICc in phylogenetic logistic regression.

4.3. Results

4.3.1 Climatic determinants of the upper critical temperature

Comparisons among single-predictor models (Table 4.2) suggest that all bioclimatic variables were more informative than the null model. Maximum temperature of the hottest month was by far the most important predictor, followed by precipitation during the warmest quarter and granivory. Data quality was uninformative in the absence of other covariates. Model-averaged estimates from the full model set (Table 4.3) included statistically significant effects of maximum temperature of the hottest month, precipitation of the warmest quarter, activity phase, log(body mass), data category 3 (UCT reported without evidence), and the two-way interaction between seasonality and migratory status. The maximum-likelihood estimate for Pagel's λ for the best model was 0.434 with a 95% confidence interval of (0.093, 0.772).

Maximum temperature of the hottest month was positively related to UCT, while precipitation of the warmest quarter, resting phase of the circadian cycle, log(body mass) and the interaction between seasonality and migratory status were negatively related to UCT (Figure 4.1). Contrary to our predictions, birds measured in the resting phase had lower UCT compared to birds measured during the active phase and the effect was significant effect.

Pearson's correlation coefficient between UCT and residuals from the best model was -0.026 and was not statistically significant, suggesting that the residuals were independent of UCT (Figure 4.2). Although negative residual values were more frequently found in the species with intermediate UCT, this can be partly attributed to the small number of species with UCT below 30ºC or above 45ºC.

4.3.2 Effect of data quality

We expected that UCT would be underestimated with low data quality because low-quality data in this dataset resulted from the lack of measurements at higher temperatures. However, contrary to expectations, model-averaged estimates indicated that UCT measurements from low quality data (category 3) were on average higher, and there was no significant difference in UCT between data categories 1 and 2 (Table 4.3). An examination of residuals by data quality category did not suggest heteroskedasticity (Figure 4.3).

When phylogenetic logistic regression was performed on the dataset including categories 1-4 (Table 4.4), three of the four models within ΔAIC<4 also contained data category as a predictor. The best model (Table 4.5) suggested, however, that this positive effect of low data quality on UCT occured only for the data category 3, and not for low-quality data overall. This model was also the model supported by backward stepwise selection. Furthermore, phylogenetic logistic regression on the binary response variable of UCT above 40ºC (Tables 4.6, 4.7) found no effect of low data quality on the probability of UCT being above 40ºC, although the final model by backwards stepwise selection included a positive effect of low data quality on UCT similar to that seen for the data quality category 3 in other datasets. Remarkably, there was little evidence of phylogenetic signal for these models, with the parameter α, defined similarly to Pagel's λ (Ives and Garland 2010), having low values of 0.020 and 0.023, respectively.

When UCT estimates from the data category 3 were excluded from the dataset, three models were within ΔAICc<4 of the best model (Table 4.8). The best model (Table 4.9) was identical to the best model for the full dataset without the effect of the data category, and was supported by AICc model averaging. The direction and magnitude of effects were generally similar, and the maximum-likelihood estimate for Pagel's λ was 0.428 with a 95% confidence interval of (0.077, 0.748), which also did not significantly differ from the estimate for the best model with all data categories included.

4.4. Discussion

4.4.1 Effects of climate and life history on avian UCT

Maximum temperature of the hottest month was the most important predictor of the upper critical temperature (Tables 4.2, 4.3; Figure 4.1). Although the moderate degree of phylogenetic signal suggests that upper critical temperatures are not highly variable across taxa in relation to environmental factors, this relationship suggests that adaptation to high maximum ambient temperatures allows the UCT to increase to some degree. Morphological (e.g., Tieleman et al. 1999, Tattersall, Andrade, and Abe 2009, van de Ven et al. 2016) and physiological (e.g., Burness et al. 2013, Nilsson, Molokwu, and Olsson 2016, Andreasson, Nord, and Nilsson 2018) adaptations that augment dry heat transfer, in addition to adaptations that facilitate efficient evaporative cooling (e.g., McKechnie et al. 2016), may allow birds in habitats with high summer temperatures to achieve smaller energetic costs of thermoregulation.

Temperate and boreal areas with high seasonality in temperature are frequently inhabited by migrants. Migration elevates basal metabolic rate due to increased amounts of energetically expensive tissue required for migration (Jetz, Freckleton, and McKechnie 2008). This increases the metabolic heat load that must be dissipated. As migrants are exposed to less extreme winter or summer temperatures, the demands for adaptation to high seasonality is likely to be reduced. The negative interaction effect between seasonality and migratory status upon upper critical temperature may represent a combined effect of increased heat load and decreased need for adaptation to high temperatures.

Water availability and humidity are high in regions with high summer precipitation, which makes it difficult to achieve effective thermoregulation while minimising water loss. When relative humidity is high, heat dissipation through cutaneous evaporative water loss is more severely reduced than that through respiratory evaporative water loss (Gerson et al. 2014). Cutaneous evaporative water loss is a more energy-efficient mechanism of evaporative thermoregulation than respiratory evaporative water loss (McKechnie and Wolf 2004). Therefore, an adaptation to dissipate metabolic heat through respiratory evaporation will result in higher metabolic rate at high temperatures. Moreover, as heat dissipation through water evaporation becomes more difficult, elevated body temperature induces higher metabolic rates (Tomlinson 2016).

We found a negative relationship between body mass and upper critical temperature. This relationship suggests that birds with large body mass tends to display low UCT. A low surface area to volume ratio results in smaller amounts of dry heat exchange, which will reduce heat dissipation when body temperature is higher than ambient temperature. Reduced body size can therefore function as an adaptive response to warm climate (Gardner et al. 2011), although this response is not universal (Goodman et al. 2012; Collins et al. 2017).

It was remarkable that UCT was lower for birds in the resting phase of the circadian cycle than in the active phase (Table 4.3; Figure 4.1). Birds in the active phase generally have higher resting metabolic rates, and their higher heat load may lead to lower UCT (McKechnie and Wolf 2004). However, studies that compared metabolism at the resting and active phase confirm that UCT is indeed lower in the resting phase (e.g., Hudson and Kimzey 1966; Hinsley et al. 1993). While the mechanism for this difference has not been examined, it is likely that certain physiological but not behavioural mechanisms are more pronounced in the active phase, resulting in higher UCT. It is noteworthy that a positive relationship between high maximum summer temperature and high evaporative water loss at high ambient temperatures occurred in active, but not resting, birds (Figure 4.1). It is possible that increase in heat dissipation by evaporative water loss is a more effective mechanism for active birds.

Examination of the residual plot (Figure 4.2) did not support the hypothesis that physiological limits constrain high UCT more strongly than low UCT. This suggests that temperate, boreal and tropical birds are likely to experience an increased energetic cost for summer thermoregulation with an increase in ambient temperatures associated with climate warming. While it has been suggested that biotic effects have a larger role in negative population trends for birds in high elevation (Milne et al. 2015), energetic challenges posed by increased costs of thermoregulation may interact with biotic effects under further climate change, especially in species with lower thermal limits and higher levels of diurnal activity. It is possible that thermal limits are even lower under field conditions because temperate and boreal regions typically show higher summer humidity than in the respiratory chambers.

4.4.2 Significance of data quality

The inclusion of low-quality data from categories 3 and 4 resulted in similar sets of predictors with identical direction of effects (Tables 4.4, 4.5, 4.7, 4.8), and the coefficient values and the standard errors, including those for Pagel's λ, were also generally similar (Tables 4.4, 4.8). However, there was a significant difference between UCT estimates from the data category 3 and estimates from other data categories. The UCT estimates from the data category 3 were considerably larger than those from other categories. It is possible that the lack of clearly defined UCT resulted in this bias. This trend, nonetheless, was not seen in any other data quality categories, including the lowest quality data in category 4, and the magnitude and direction of this effect is also difficult to address.

The 28 species that comprised data category 3 were mostly from humid tropical regions of the southern hemisphere, with high annual mean temperature, high annual precipitation and low seasonality in temperature (Figure 4.4). UCT estimates for 23 of the 28 category 3 species were obtained from relatively few captive-raised individuals (McNab 2000, 2001, 2003; McNab and Ellis 2006). Unfortunately, good-quality UCT measurements are scarce for birds of humid tropical regions (Figure 4.5). There is insufficient information on differences between captive and wild birds in their responses to high ambient temperature.

Overall, while UCT estimates from data category 3 were significantly higher than those from other data categories, several confounding factors are present in these studies that obscure the effect of poor data quality on estimating the relationship between UCT and environmental predictors. Piecewise linear regression, used frequently to estimate points of change in the slope of a linear relationship, often performs poorly even in relatively high-quality data. It is possible that estimates by such methods are, on the whole, not more precise or accurate than attempting to determine whether the animal has reached UCT by a combination of metabolic rate measurements and other aspects of the behaviour and physiology of the animal. The presence of potential confounders, along with the low performance of piecewise linear regression, make it difficult to dismiss the claim that the relationship between thermal variables and environmental covariates are robust to the issues of poor data quality (Hof et al. 2017). There are relatively few studies that include high-quality data, and a large proportion of the dataset comprise of species in warm, arid habitats (Figure 4.5). It will be beneficial to collect metabolic measurements across a wide range of temperature from birds that inhabit boreal and humid tropical areas.

Table 4.2. Correlation for climate predictors initially selected to be included in the model. T_{mean}=annual mean temperature, T_{seas}=temperature seasonality(standard deviation), T_{max}=maximum temperature of the hottest month, T_{range}=annual temperature range, T_{summer}=mean temperature of the hottest month, P_{ann}=annual precipitation, P_{seas}=precipitation seasonality(standard deviation),, P_{warm}=precipitation of warmest quarter. Values in bold face are significant after Bonferroni correction for multiple comparison.

	T_{mean}	T_{seas}	T_{max}	T_{range}	T_{summer}	P_{ann}	P_{seas}	P_{warm}
T_{mean}	1.00							
Ts_{eas}	**-0.69**	1.00						
T_{max}	**0.70**	0.00	1.00					
T_{range}	**-0.57**	**0.95**	0.19	1.00				
T_{summer}	**0.81**	-0.14	**0.96**	-0.02	1.00			
P_{ann}	**0.31**	**-0.59**	**-0.25**	**-0.71**	-0.06	1.00		
P_{seas}	0.14	**0.24**	**0.45**	**0.34**	**0.36**	**-0.45**	1.00	
P_{warm}	**0.24**	**-0.41**	-0.17	**-0.53**	-0.01	**0.91**	**-0.38**	1.00

Table 4.3. Single-predictor models from data categories 1-3.

Predictor	Log-likelihood	AICc	ΔAICc
Maximum temperature of the hottest month	-234.76	473.59	0
Precipitation of the warmest quarter	-240.85	485.76	12.17
Granivory	-241.87	487.81	14.22
Long-distance migration	-243.81	491.69	18.10
Temperature seasonality	-244.44	492.95	19.36
Activity phase	-244.57	493.21	19.62
log(body mass)	-244.81	493.69	20.10
(null)	-247.21	496.44	22.85
Data category	-245.29	496.71	23.12

Table 4.3. Model-averaged coefficient estimates for the data categories 1-3.

Predictor	Estimate	SE	p	cumulative AICc weight
maximum temperature of the hottest month	0.294	0.067	<0.001	1
temperature seasonality	0.006	0.119	0.959	1
long-distance migration	0.140	0.256	0.586	0.98
precipitation of the warmest quarter	-0.176	0.079	0.028	0.84
activity phase ρ	-0.365	0.134	0.007	0.94
log(body mass)	-0.239	0.096	0.013	0.89
Data category 2	-0.113	0.139	0.414	0.77
Data category 3	0.439	0.220	0.046	0.77
temperature seasonality*long-distance migration	-0.568	0.178	0.001	0.96

Table 4.4. Models within ΔAIC < 4 from the best model for the binary response of UCT>35ºC. T_{max} = maximum temperature of the hottest month, T_{seas}=temperature seasonality(standard deviation), P_{warm}=precipitation of the warmest quarter.

coefficients	AIC	ΔAIC	weight
T_{max}+T_{seas}*long-distance migration+P_{warm}+phase+data category	232.10	0.00	0.42
T_{max}+T_{seas} *long-distance migration+P_{warm}+phase+log(body mass)+data category	234.17	2.07	0.15
T_{max}+T_{seas} +P_{warm}+phase+log(body mass)+data category	235.12	3.02	0.09
T_{max}+T_{seas} *long-distance migration+ P_{warm} +phase	235.73	3.63	0.07

Table 4.5. Best model for the binary response of UCT>35ºC. p-values are obtained by the Wald approximation.

coefficient	Estimate	SE	p	cumulative weight	AIC
Maximum temperature of the hottest month	0.551	0.159	<.001		1
Long-distance migration	1.587	0.704	0.024		0.74
Temperature seasonality	-0.106	0.228	0.642		1
Precipitation of the warmest quarter	-0.263	0.167	0.116		0.94
Activity phase ρ	-0.87	0.339	0.01		0.94
data category 2	-0.158	0.343	0.644		0.83
data category 3	0.995	0.529	0.06		0.83
data category 4	0.053	0.103	0.918		0.83
Temperature seasonality*long-distance migration	-1.225	0.545	0.025		0.69

Table 4.6. Models within ΔAIC < 4 from the best model for the binary response of UCT>40ºC. T_{max} = maximum temperature of the hottest month, T_{seas}=temperature seasonality(standard deviation).

model	AIC	ΔAIC	weight
T_{max}+ T_{seas} +phase+log(body mass)	144.61	0.00	0.31
T_{max}+phase	145.45	0.84	0.20
T_{max}+phase+log(body mass)	146.22	1.61	0.14
T_{max}+phase+long-distance migration	146.69	2.08	0.11
T_{max}+ T_{seas} +phase	147.14	2.53	0.09
T_{max}+phase+long-distance migration+log(body mass)	147.31	2.70	0.08

Table 4.7. Best model for the binary response of UCT>40ºC. p-values are obtained by the Wald approximation.

Predictor	Estimate	SE	p	cumulative weight	AIC
maximum temperature of the hottest month	0.478	0.129	<.001		1
activity phase ρ	-0.615	0.212	0.004		1
temperature seasonality	0.134	0.093	0.148		0.47
log(body mass)	0.143	0.139	0.304		0.53

Table 4.8. Best model for the dataset including data categories 1-2.

predictor	Estimate	SE	p	cumulative weight	AICc
maximum temperature of the hottest month	0.301	0.074	<.001		1
temperature seasonality	0.029	0.111	0.793		1
long-distance migration	0.105	0.243	0.666		0.98
precipitation of the warmest quarter	-0.153	0.079	0.055		0.71
activity phase ρ	-0.23	0.098	0.021		0.93
log(body mass)	-0.373	0.137	0.007		0.83
temperature seasonality*long-distance migration	-0.586	0.179	0.001		0.96

Figure 4.2. The relationship between UCT and significant predictors. Data points marked in red belong to the data category 1, those marked in green belong to the category 2 and those in blue belong to the category 3. In the top right image, triangles mark long-distance migrants.

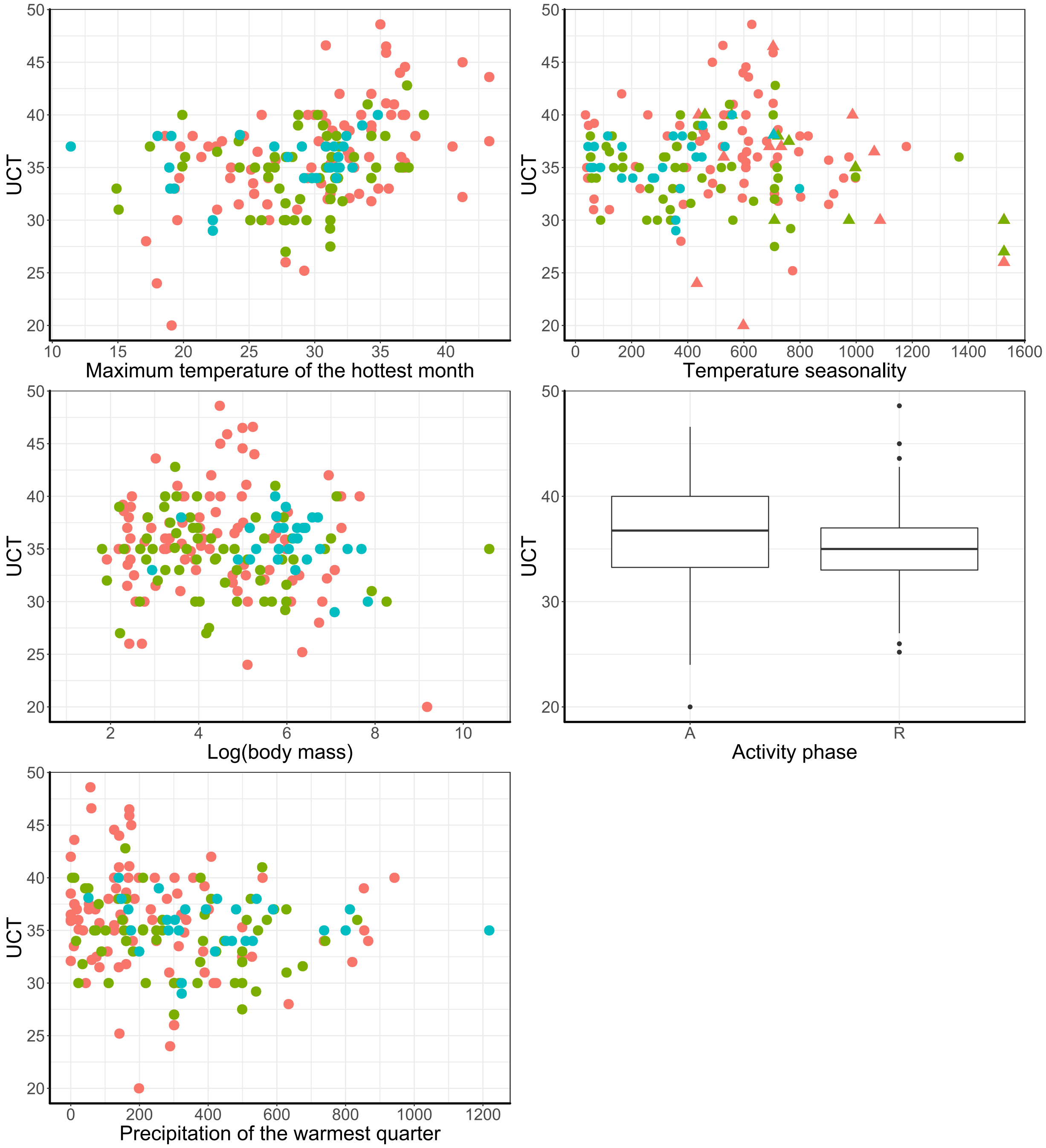


Figure 4.3. The residual plot for UCT

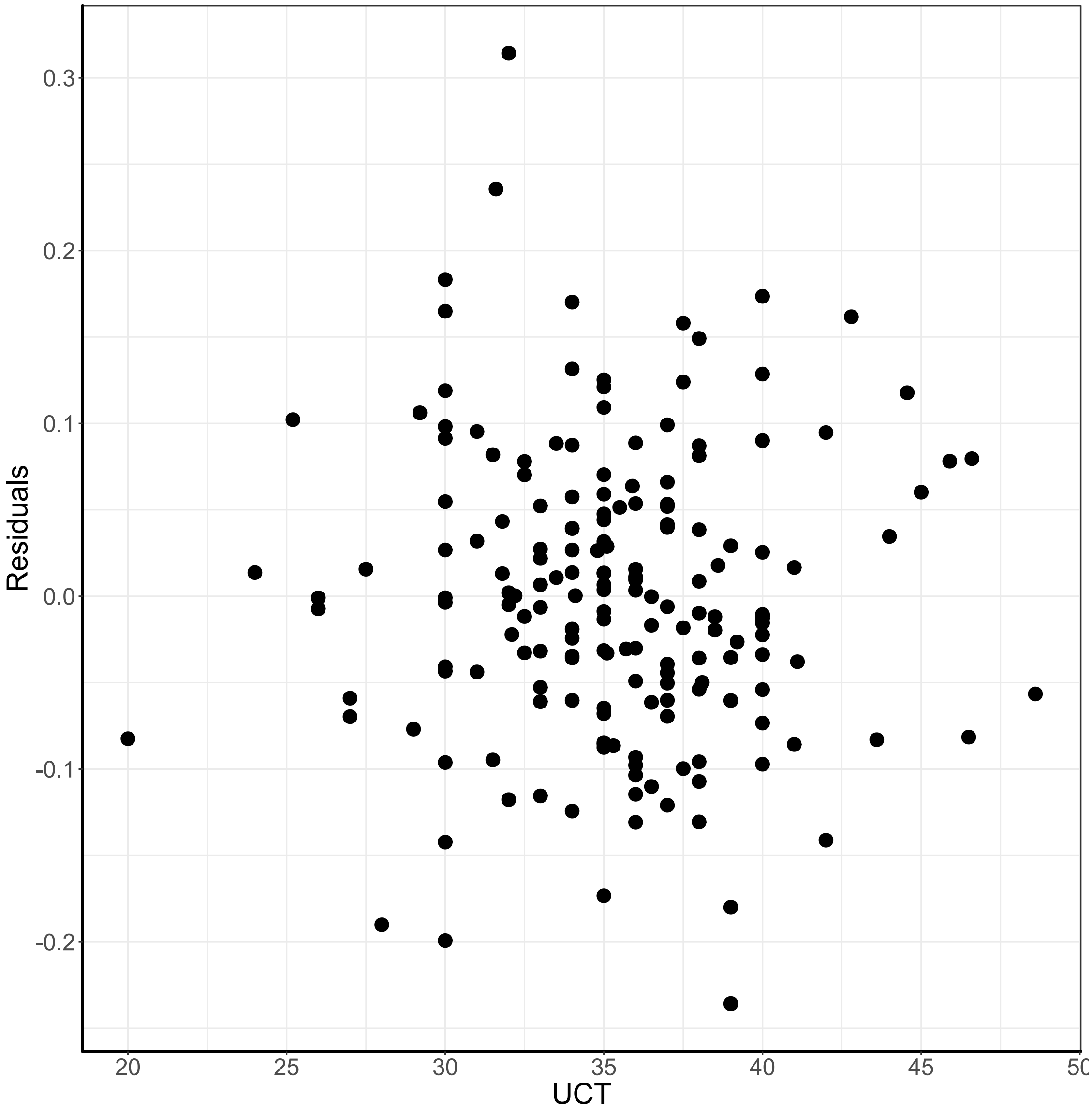


Figure 4.4. Residuals for the three data categories

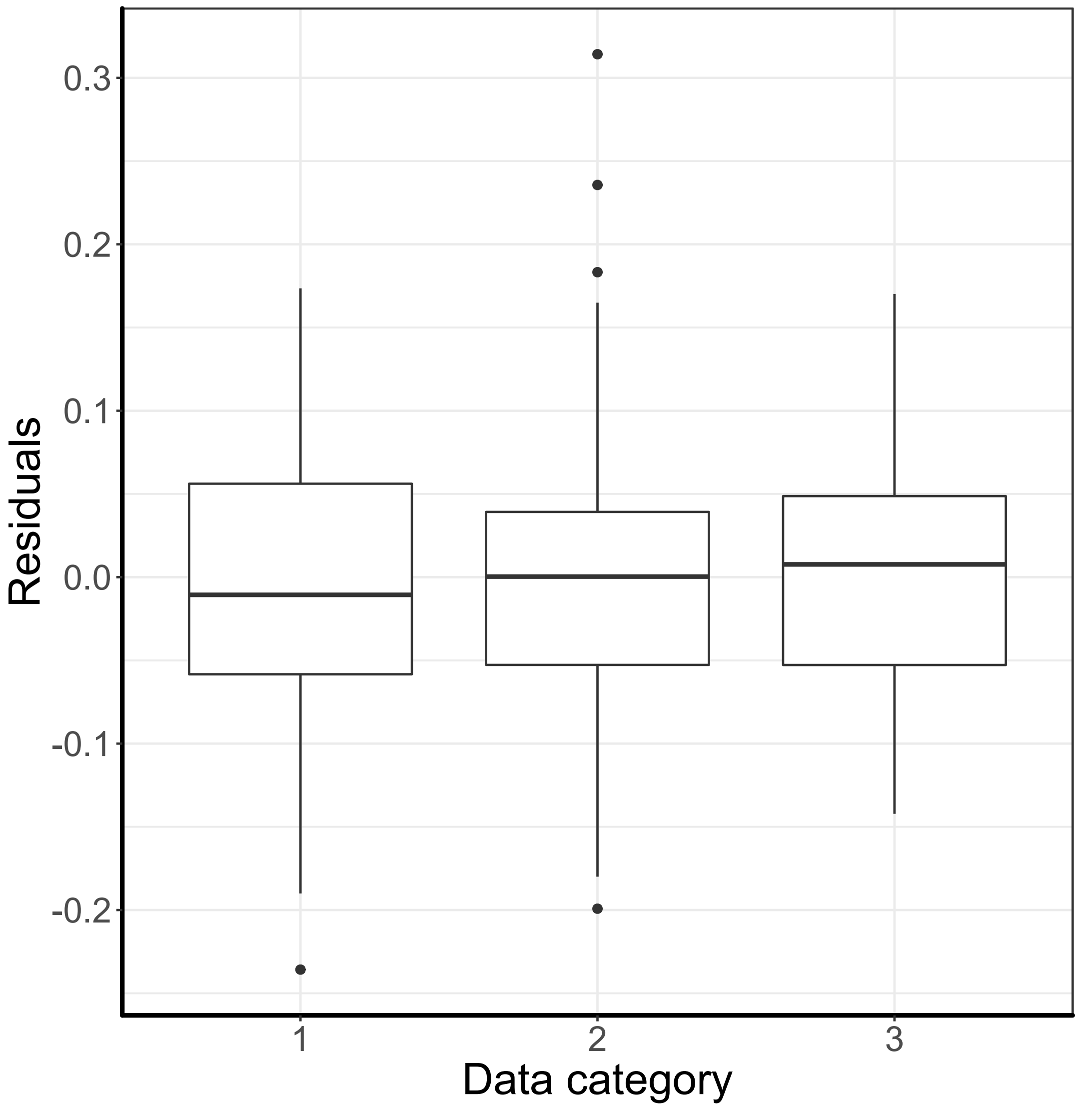


Figure 4.5. The annual temperature, precipitation and temperature seasonality for different data categories

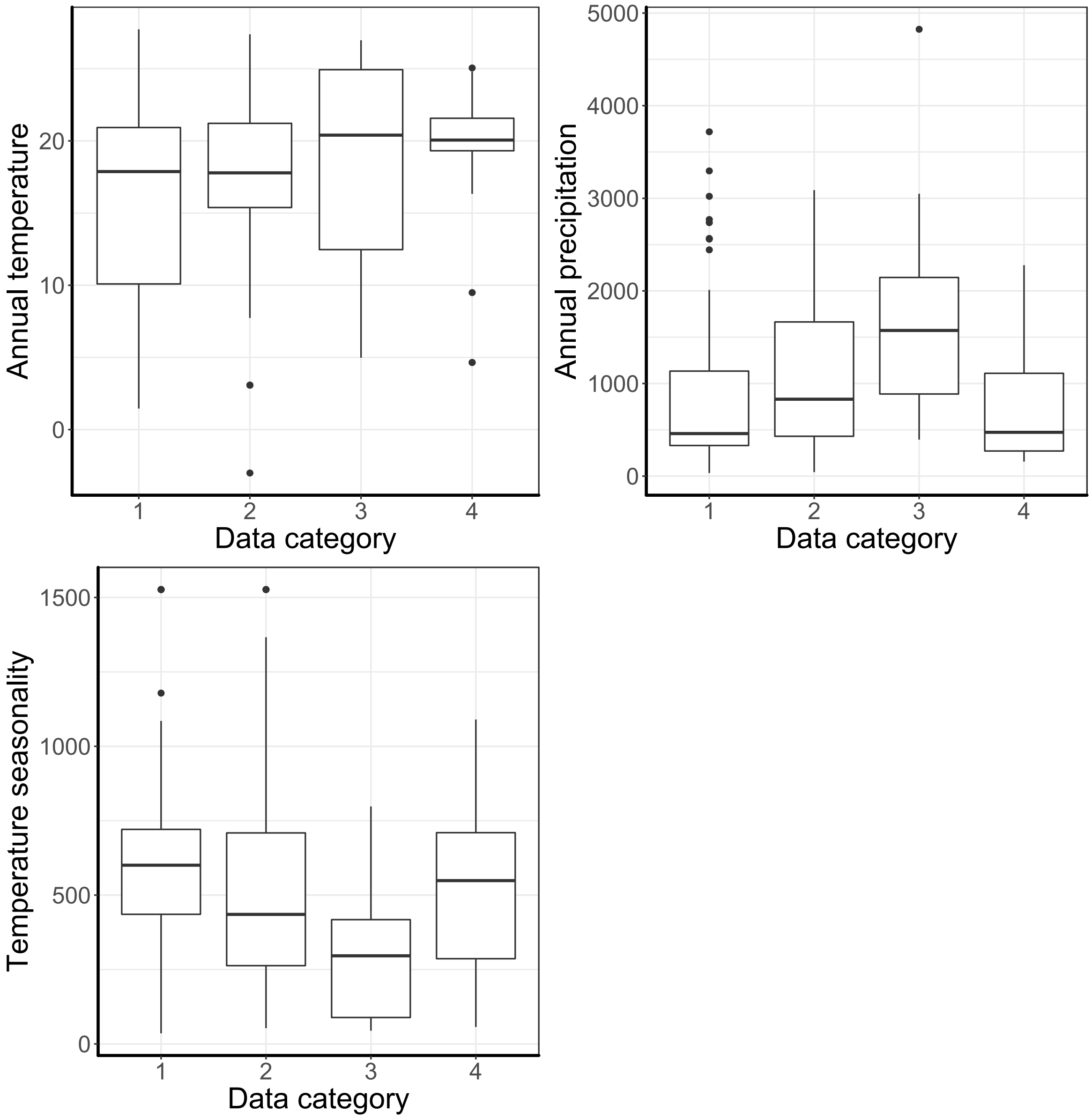
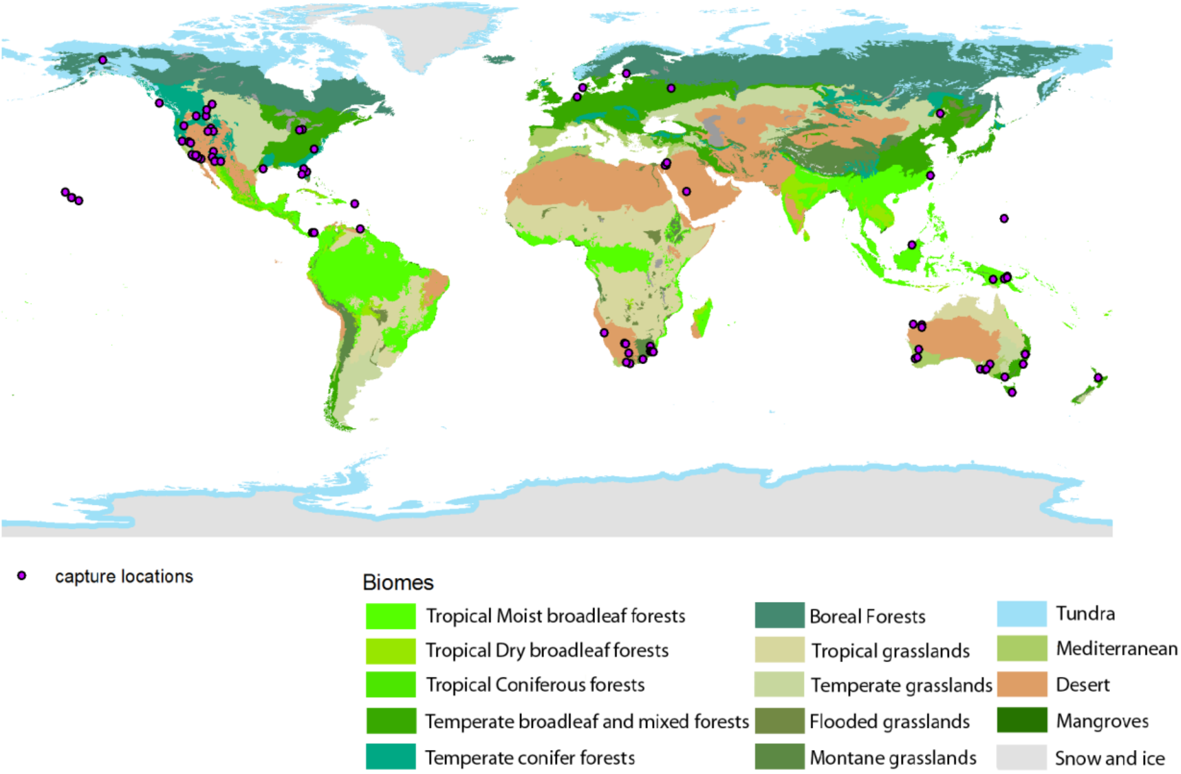


Figure 4.S1. Capture locations for the species included in the study.



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