Generalized evidence for Bergmann's rule body size variation in a cosmopolitan owl genus

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Short title: Bergmann's rule in a cosmopolitan owl

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Abstract

Aim. The eco-geographic Bergmann's rule predicts that animals have smaller body size in warmer regions than in cold environments because of thermoregulatory reasons. Although this rule has been widely investigated, intraspecific analyses on cosmopolitan taxa are rare. We examined whether geographic variation in wing length, a proxy of body size, shows a Bergmannian pattern and can be explained by three mechanisms known to affect animal body size (heat conservation, resource availability and starvation resistance) in seven species of nocturnal raptors of the genus *Tyto*.

Location. World.

Taxon. Genus *Tyto*.

Methods. We measured wing length of 9033 museum specimens covering the entire distributional range of each species and linked it with geographic (absolute latitude, elevation) and climatic predictors associated with heat conservation, resource availability and starvation resistance hypotheses of spatial variation in body size.

Results. All the species show a trend of increasing wing length with increasing latitude and/or elevation, and in five of them either or both geographic predictors are statistically significant. In all the species showing a Bergmannian pattern, wing length significantly decreases with temperature, thus supporting the heat conservation hypothesis. Conversely, we found less generalized support for the other hypotheses, although in some species significant trends between wing length and proxies of climatic seasonality and/or primary productivity emerged.

Main conclusions. Consistent clines in body shrinking in warm environments are observed in species living in different continents at different latitudinal and temperature ranges, as well as exploiting different habitats. These findings thus support the hypothesis that body size is, at least partly, selected for heat maintenance depending on the thermal environment, even in nocturnal species which are not directly exposed to solar radiation. However, different selective pressures may also have concomitantly acted to promote body size evolution in this bird group.

Keywords: Bergmann's rule, body size, biogeographical rules, convergent evolution, cosmopolitan species, thermoregulation, *Tyto*

Introduction

The tendency of animals to have larger body size in cooler regions (i.e. higher latitudes and elevations) than in those characterized by warm climates has been generalized with the name of "Bergmann's rule" (Bergmann, 1847; Rensch, 1936), after the first scientist who recognized such a general pattern. The ultimate explanation to interpret clines in animal body sizes compatible with this rule is based on heat conservation. Specifically, larger bodies are favoured in cold environments because the lower surface to volume ratio limits heat dissipation, thus resulting in an expected improvement in the survival chances (Mayr, 1956; 1963). The opposite holds true in warm climates, where smaller body sizes should be positively selected for the opposite reason. The size of the body can be therefore considered as a thermoregulatory adaptation to cope with different climatic conditions. Being conceived for endotherms, where patterns coherent with such a prediction have been observed in a plethora of taxa in many regions of the globe (e.g. Brown & Lee, 1969; Ashton et al., 2002; Meiri & Dayan, 2003; Ashton, 2004, Rodríguez et al., 2006; Meiri et al., 2007; Olson et al., 2009; Torres-Romero et al., 2016; Gibson et al., 2019), recent studies have confirmed the validity of this biogeographical rule also in some ectotherms (e.g. Arnett & Gotelli, 1999, Ashton & Feldman, 2003; Olalla-Tárraga et al., 2006, 2007; Chown & Gaston 2010; Pallarés et al., 2019). Nevertheless, many exceptions have been reported (e.g. Ashton & Feldman 2003, Olalla-Tárraga et al., 2006, 2007; Slavenko & Meiri 2015; Nunes et al., 2016; Freeman, 2017; Medina et al., 2017; Sargis et al., 2018), and there is still a vibrant debate about which taxonomic level should the rule be applied to according to Bergmann's original formulation and whether interspecific and intraspecific patterns represent two different phenomena or follow the same rules (Blackburn et al., 1999; Olson et al., 2009; Meiri & Thomas, 2007; Watt et al., 2010; Meiri, 2011; Salewski & Watt, 2017). Although many studies investigated Bergmann's rule by comparing phylogenetic closely related species, or even species assemblages, recent theoretical studies suggested that this rule should be stronger at the intraspecific level (Meiri & Thomas, 2007; Watt et al., 2010; Meiri, 2011; Salewski & Watt, 2017; but see Olson et al., 2009).

It is important to note, however, that body size is a composite trait, which is associated with a large suite of diverse functions, and latitudes and elevations are also both linked to several environmental factors (and variation in them) other than temperature. Indeed, the validity of heat conservation mechanism (hereafter *heat conservation hypothesis*) has been challenged, primarily because of the existence of many morphological adaptations, like changes in fur or feathers and the presence of a thick fat layer, which can have greater importance in affecting heat gain and loss (Scholander, 1955; Irving, 1957; McNab, 1971). In addition, studies of both ectotherms and endotherms have challenged the generality of the mechanism underpinning the Bergmann's rule (e.g. Geist, 1987; McNab, 1971; reviewed in James, 1970; Blackburn et al., 1999; Meiri & Dayan, 2003; Meiri & Thomas, 2007; Watt et al., 2010), and other hypotheses have proven valid to explain geographic variation in body size of some animal taxa (e.g. Blackburn & Hawkins, 2004; Jones et al., 2005; Rodríguez et al., 2006; Olalla-Tárraga et al., 2006, 2007; Ramirez et al., 2008; Diniz-Filho et al., 2009; Olson et al., 2009; Morales-Castilla et al., 2012). The *resource availability hypothesis* states that body size is expected to increase with increasing availability of resources, rather than with decreasing temperatures, because primary productivity sets a limit to the body sizes animals can reach (Rosenzweig, 1968; Geist, 1987). Moreover, the *starvation resistance hypothesis* argues that larger animals are favoured in seasonal environments characterized by variable ecological conditions because they can survive starvation better than smaller ones (Lindsey, 1966; Boyce, 1978; Lindstedt & Boyce, 1985). According to these hypotheses, variation in body size may not strictly follow geographical clines in the direction predicted by the Bergmann's rule (i.e. larger body size at high latitudes and elevations). Finally, the *dispersal ability hypothesis* proposes that a large body size at high latitudes is the result of lower dispersal ability of smaller animals which have failed to fully re-colonize deglaciated areas after the Pleistocene (Blackburn & Gaston, 1996; Newton & Dale, 1996). However, these hypotheses are non-mutually exclusive and several studies showed that different mechanisms can simultaneously act to generate predictable Bergmannian patterns of body size variation along geographical gradients (e.g. Jones, 2005; Ramirez et al., 2008; Olson et al., 2009; Morales-Castilla et al., 2012)

In birds, geographic variation in body size compatible with Bergmann's rule has been shown in comparative studies including both single species and species assemblages (e.g. Blackburn & Ruggiero, 2001; Ashton et al., 2002; Meiri & Dayan, 2003; Ashton, 2004; Olson et al., 2009; Meiri, 2011; Blackburn et al., 2019) and at the within-species level on a continental geographical scale (e.g. James, 1970; Graves, 1991; Jones et al., 2005; Fan et al., 2019; Gibson et al., 2019). However, comprehensive intraspecific analyses on cosmopolitan taxa are almost null (but see Murphy, 1985). This is unfortunate because species with wide geographical distributions provide the possibility to compare populations living in distinct environments characterized by very different climatic and ecological conditions, which is precluded by single taxon studies, without the need to account for many confounding evolutionary factors, as it is the case for multi-taxa studies.

The aim of the present study is to examine whether the variation in body size in different species of the genus *Tyto* (family Tytonidae), a cosmopolitan group of nocturnal raptors, is coherent with Bergmann's rule, while testing for different potential mechanisms known to affect body size in birds. To this purpose, we used more than 9000 specimens collected in the entire range of distribution of seven species showing at least a continental distribution range (Figure 1; see Methods for details). Such an approach allows us to examine whether the same associations between body size, geography and climate are convergently observed in geographically separated regions, by comparing size clines between taxa showing different distribution ranges and inhabiting different continents and latitudes (see also Ashton, 2004; Meiri et al. 2007).

We firstly described the geographical variation in body size of the seven aforementioned taxa to examine whether it varies with latitude and elevation in a way compatible with the scenario predicted by Bergmann's rule. We then investigated whether geographic patterns in body size can be explained by climatic proxies associated with the *heat conservation hypothesis*, the *resource availability hypothesis* and the *starvation resistance hypothesis*. We did not test the *dispersal ability hypothesis* because it mainly refers to interspecific differences. In addition, however, four species included in our study occupy a range which was not affected by glaciations, and the remaining ones (i.e. the three lineages of the *T. alba* species complex) are composed by populations which re-colonized the glaciated regions (but only the very Northern part of their current distribution range; Antoniazza et al. 2010) and other ones living in non-glaciated areas, thus making such a hypothesis untestable on our study system.

Methods

Study species

Three taxa included in our analyses belong to the cosmopolitan common barn owl (previously known as *Tyto alba*) species complex. Although their taxonomic status has to be elucidated fully, all the phylogenetic studies available to date (Aliabadian et al., 2016; Uva et al., 2018; Wink et al., 2009) are coherent in agreeing that this species complex is divided into three genetically distinct evolutionary lineages, living in geographically separated areas and showing a considerable genetic differences among each other: the Western (or Afro-European) barn owl (*T. alba*), occurring from southern Scandinavia to South Africa, including Arabian Peninsula, Middle East, Madagascar, and all the African archipelagos in the Atlantic and Indian Oceans, the American barn owl (*T. furcata*), from southern Canada to Patagonia, including most of islands in the Pacific and Atlantic Oceans (e.g. Caribbean, Hawaii, Galapagos and Falkland), and the Eastern (or Australasian) barn owl (*T. javanica*), from the Himalayan plateau to Tasmania, including most archipelagos in the Australasia and in the Pacific Ocean (see Figure 1; Romano et al., 2019 for details). These taxa can exploit a wide range of habitats, from open landscapes like deserts and grasslands to temperate and tropical forests, thus allowing them to occur across huge latitudinal ranges.

The other species included in the study are: the African grass owl (*T. capensis*), living in moist grasslands and open savannas located in the Africa south of the Equator; the Australasian grass owl (*T. longimembris*), inhabiting in open habitats (mainly grasslands) from southern China and India to southern Australia, including many islands in the region; the Australian masked owl (*T. novaehollandiae*), which is distributed along the Australian coasts and Tasmania, but also in the Southern New Guinea and in some Australian islands in the Timor Sea and it mostly lives in forested habitats; and the sooty owl group (*T. tenebricosa-multipunctata*), limited to moist dense forests located in New Guinea and on the east coast of Australia (Figure 1).

Our analyses therefore include all the species of the *Tyto* genus showing at least a continental distribution, thus discarding only few taxa present in single islands (*T. soumagnei* from Madagascar, *T. inexpectata* from Sulawesi, *T. aurantia* from New Britain island; see Uva et al., 2018 for details).

According to the most recent and comprehensive phylogenetic analysis (Uva et al., 2018), two out of the seven taxa considered here, namely *T. furcata* and *T. javanica*, might be paraphyletic because they include other formerly recognized species with insular distribution. In particular, the ashy-faced owl (*T. glaucops*) from Hispaniola and lesser Antilles islands is nested within *T. furcata*, while the Sulawesi masked owl (*T. rosenbergii*) and the Taliabu masked owl (*T.

nigrobrunnea) are both embedded within *T. javanica* (Uva et al., 2018). The analyses were therefore performed both including and excluding data of these three insular taxa within *T. furcata* or *T. javanica*.

In addition, there is large controversy about the taxonomic level of the greater and lesser sooty owls (*T. tenebricosa* and *T. multipunctata*), which have been considered as either conspecifics or two different species depending on the criteria adopted. However, from a genetic point of view, they are very closely related, as the evolutionary divergence was recently estimated in only 0.6% (Uva et al., 2018). Again, the analyses were performed both excluding and including individuals of *T. multipunctata* because distribution of this species is confined to a smaller geographic area (Figure 1) and because of the much smaller sample size (29 vs. 71 specimens). Finally, the genetic divergence between the African and the Australasian grass owls (*T. capensis* and *T. longimembris*) is also limited, thus suggesting that they might not be two separate species. However, their large geographic isolation (Figure 1) prevented us from analysing these two taxa in a single statistical model.

Finally, all the taxa are considered resident. However, some migration has been observed in sexually-mature birds in a population of *T. furcata* living at the northernmost limit of its range distribution (Duffy & Kerlinger, 1992). However, when the analyses described below were repeated excluding this population the results were qualitatively unchanged (details not shown). In addition, although not migrant, *T. longimembris* is mostly a nomadic species (Clulow et al. 2011).

Museum skins collection and measurement

Following the vast majority of the studies investigating body size variation in birds (see e.g. a meta-analysis by Ashton, 2002), we used wing length as proxy for body size (Meiri, 2003; Salewski & Watt, 2017). In addition, since we relied only on museum specimens, wing size is the most available and reliable osteometric information that was possible to collect.

Wing length of 9033 Tytonidae specimens, collected between the years 1809 and 2019 by 148 museums and private citizens, was measured by the same experimenter (i.e. Alexandre Roulin). Collected skins cover the entire range of distribution of the analyzed taxa, and the total sample included: 4057 *T. alba*, 2684 *T. furcata* (plus 118 specimens of *T. glaucops*), 1243 *T. javanica* (plus 37 specimens of *T. rosenbergii* and 1 specimen of *T. nigrobrunnea*), 181 *T. capensis*, 201 *T. longimembris*, 411 *T. novaehollandiae*, 100 *T. tenebricosa-multipunctata* group (71 *T. tenebricosa* and 29 *T. multipunctata*) specimens (Figure 1).

Climatic and geographic information

Locations where specimens were collected were converted into latitude and longitude coordinates. If the museum label reported a region, an island or small country name, rather than an exact location, we assigned coordinates near the centre of the specified region. For each pair of coordinates, we collected information on elevation and climatic information linked to different hypotheses to be tested.

The *heat conservation hypothesis* was tested using mean annual temperature as a proxy, collected at a 30 arc-second spatial resolution from the Worldclim dataset for the period 1970–2000 (Fick & Hijmans, 2017). Such a timespan is a good proxy for the climatic variables recorded in the entire timespan where specimens were collected (see Romano et al., 2019, 2020a). In addition, however, variation in the body size and the size of different body parts have often been linked to the minimum or the maximum temperature recorded in a year, rather than to the mean annual temperature (e.g. Rodríguez et al., 2008; Danner & Greenberg, 2015; Fan et al., 2019). Therefore, we also extracted information on the minimum temperature of the coldest month and maximum temperature of the warmest month.

The *resource availability hypothesis* was tested using mean annual actual evapotranspiration as a proxy of primary productivity (Rosenzweig, 1968; Jones et al., 2005; Olalla-Tárraga et al., 2006; Morales-Castilla et al., 2012). Actual evapotranspiration data were collected at a 30-seconds spatial resolution, from the Global High-Resolution Soil-Water Balance dataset for the period 1950-2000 (Trabucco & Zomer, 2010).

The *starvation resistance hypothesis* (also called the *seasonality hypothesis*; Blackburn et al., 1999; Watt et al., 2010) was originally proposed for highly seasonal habitats (Lindsey 1966). Following previous studies (e.g. Boyce, 1978; Lindsted & Boyce, 1985; Murphy, 1985; Zeveloff & Boyce, 1988; Jones et al., 2005), it was tested using the temperature annual range extracted from Worldclim dataset for the period 1970–2000 (Fick & Hijmans, 2017) as a proxy of the within-year variability in climatic and ecological conditions.

Importantly, individuals of the species included in our analyses are generally territorial and usually spend the entire year within few km from their breeding site, potentially exploiting different habitats. We therefore associated to each individual the mean values of the climatic/ecological variables mentioned above (including elevation) over a radius of 20 km from the location where each specimen was collected (see Romano et al., 2019, 2020a). This procedure is also useful to account for small errors in the identification of the recovery site reported in the museum labels, and when the information on the specimen recovery location was not precise (see also Gibson et al., 2019).

We note that the timespan of climatic data does not coincide with the period when the specimens were collected (1809–2019). However, in spite of the climate change in the last century, similar climatic differences have persisted between regions. We indeed showed that temperature information collected in the period 1970–2000 is highly correlated ($r > 0.92$) with the temperature recorded in the same locations in various time windows during the past 20,000 years (see Romano et al., 2019, 2020a, 2020b), and it is therefore a valid measure to investigate whether body size variation follows Bergmann's rule in this bird genus.

In addition, we did not include the collection year of the specimens in the main analyses because different regions were not equally sampled across time (e.g. most of the owls originating from Indonesia and Papua New Guinea were collected during the European colonization of these countries). An eventual significant effect of collection year would therefore mainly reflect a geographic variation in sampling across time rather than a 'real' temporal effect. However, when the analyses were repeated on the subsample of individuals for which the year of collection was known, we obtained qualitatively similar results to those presented below (details not shown).

Statistical analyses

To examine variation in wing length according to Bergmann's rule and to test for possible mechanisms in explaining geographical trends we used generalized linear models with the glmmTMB package (Brooks et al., 2017) in R (version 3.5.1). We firstly performed descriptive models to examine whether geographic variation in wing size is compatible with Bergmann's rule separately for each taxon. We included as predictors absolute latitude and log-transformed elevation, as well as, when necessary (i.e. if a given taxon lives in both hemispheres), a dichotomic factor indicating if the specimen was collected in the northern (coded as 1) or in the southern (coded as 2) hemisphere. Given that for *T. alba* and *T. furcata* some birds were recovered below sea level, the logarithmic conversion was performed after the addition of the most negative elevation value of each lineage to all elevation values of the corresponding lineage. This procedure thus generated all positive elevation values and helped to maintain the absolute elevation difference among locations.

We then performed four separate models for each taxon in order to test for different hypotheses of body size variation in space. These models included as predictors 1) mean annual temperature (*heat conservation hypothesis*), 2) minimum and maximum annual temperature (*heat conservation hypothesis*), 3) actual evapotranspiration (*resource availability hypothesis*), and 4) temperature annual range (*starvation resistance hypothesis*). Because body size may not always vary monotonically with temperature (see e.g. Rodríguez et al., 2008; Morales-Castilla et al., 2012; Blackburn et al., 2019), in the first model of the above list we also included the quadratic term of temperature, which was removed from final models because it never reached statistical significance (details not shown).

In addition, because body size is expected to vary between insular and continental populations (Lomolino, 2005), and this is the case also for the Tytonidae (Roulin & Salamin, 2010), in the analyses we considered if individuals originated from islands or mainland by including a two-level factor (island coded as 1; mainland coded as 0) when a taxon is present both on islands and mainland (including Australia). This was the case for all the taxa with the exception of *T. capensis*. Importantly, to account for non-random distribution of recovery locations (i.e. to account for data spatial autocorrelation), in all the models we added an exponential correlation structure considering the distances between all the pairs of latitude-longitude coordinates.

Because all the analyses of a single species were run on the same sample of individuals, we compared the associated Akaike information criterion (AIC) of the different models within each species in order to identify the most supported one. Finally, all the analyses were performed by standardizing all the variables, including the dependent variable. Under such circumstance, the regression coefficients strictly reflect the strength of the association between the dependent variable and each predictor (Schielzeth, 2010; see also Romano et al. 2020a). These values were thus used to directly compare the effects of different predictors on the variation in wing length within a single species, as well as the effects of the same climatic predictor on different species.

Results

In all the taxa with the exception of *T. alba* and *T. longimembris*, wing length significantly varies with absolute latitude and/or elevation in a way coherent with the prediction of Bergmann's rule (Table 1). Indeed, wing length significantly and positively covaries with absolute latitude in four species, namely *T. furcata, T. capensis*, *T. novaehollandiae* and *T. tenebricosa-multipunctata*, while in *T. javanica*, *T. capensis* and *T. furcata* with elevation. Thus, the two species showing both and positive trends with latitude and elevation are the African *T. capensis* and the American *T. furcata*. Very similar results to those reported in Table 1 were obtained for *T. furcata* when the analyses were performed excluding data of *T. glaucops* (latitude: 0.363 ± 0.161; t = 2.25; P = 0.025; elevation: 0.075 ± 0.025; t = 3.11; P = 0.002), and *T. javanica* excluding data of *T. rosembergii* and *T. nigrobrunnea* (latitude: -0.036 ± 0.185; t = -0.19; P = 0.85; elevation: 0.092 ± 0.028; t = 3.25; P = 0.001).

In all the species showing a significant Bergmannian geographic variation in wing length, we also observed a significant negative relationship between wing length and mean annual temperature (Table 2a; Figure 2) in line with the *heat conservation hypothesis*. Although in *T. alba* and *T. longimembris* this relationship is statistically non-significant, the trend is also negative

(Table 2a; Figure 2). Similar results were obtained when in *T. furcata* were excluded data of *T. glaucops* (coefficient ± SE: -0.107 ± 0.037; t = -2.89; P = 0.004), in *T. javanica* data of *T. rosembergii* and *T. nigrobrunnea* (coefficient ± SE: -0.207 ± 0.076; t = -2.71; P = 0.007), and in *T. tenebricosa* data of *T. multipuncatata* (coefficient ± SE: -0.319 ± 0.135; t = -2.7381; P = 0.018).

Interestingly, in all the species for which mean annual temperature is a significant predictor of wing length, this is also the case for minimum annual temperature (Table S1). In addition, this climatic variable significantly and negatively predicts wing length in *T. alba* (Table S1). Thus, in six out of the seven species included in our analyses wing length negatively covaries with minimum annual temperature, while maximum annual temperature is significantly associated with wing length only in *T. novaehollandiae* (Table S1).

More complex are the results about the association between wing length and actual evapotranspiration (Table 2b; Figure S1). Indeed, in *T. alba* and *T. javanica* wing length significantly increases with increasing actual evapotranspiration, as predicted by the *resource availability hypothesis*. In the species showing non-significant trends, the sign of the relationship between wing length and actual evapotranspiration is variable, thus indicating that this result is difficulty generalizable. Similar results were obtained for *T. furcata* excluding data of *T. glaucops* (t = 0.62; P = 0.53), *T. javanica* excluding data of *T. rosembergii* and *T. nigrobrunnea* (t = 2.36; P = 0.018), and *T. tenebricosa* excluding data of *T. multipuncatata* (t = 0.09; P = 0.93).

Conversely, for all the species the covariation between temperature annual range and wing length is positive, as predicted by the *starvation resistance hypothesis* (Table 2c; Figure S2). However, with the only exception of *T. tenebricosa-multipuntata*, all the trends are not statistically significant. Again, results were qualitatively similar excluding *T. glaucops* in *T. furcata* (t = 1.44; P = 0.15), as well as *T. rosembergii* and *T. nigrobrunnea* in *T. javanica* (t = 0.56; P = 0.58) and *T. multipuncatata* in *T. tenebricosa* (t = 4.38; P < 0.001).

We finally repeated all the analyses above on a subsample of specimens of *T. novaehollandiae* and *T. furcata* in order to check for the solidity of our results after the removal of some specific individuals. In particular, analyses of *T. novaehollandiae* were repeated excluding the 10 individuals collected in Lord Howe Island, where the species was introduced in the 1920s to the purpose of eradicating allochthonous rodents which were threatening the populations of endemic species (Milledge et al., 2019). The results were very similar to those shown in Tables 1 and 2 (details not shown), thus indicating that the inclusion of this introduced population did not affect the results. Moreover, it is possible that variation in wing size according to temperature in *T. furcata* might have been affected by the distribution of island populations, where owls are considerably smaller (see Tables 1 and 2), which are mostly found close to the Equator and therefore in warm climates (see Figures 1 and 2). However, when the analyses were repeated on continental specimens only, the results were confirmed (mean annual temperature: $t = -2.82$; $P = 0.005$; minimum temperature: $t = -2.36$; $P = 0.018$).

Discussion

Our study shows a consistent variation in wing length, a reliable proxy of body size in birds, according to temperature in different species of the cosmopolitan *Tyto* genus. Indeed, five out of the seven investigated species showed a significant decrease in size with increasing temperature, a percentage similar to that reported by previous comparative studies (Ashton, 2002; Meiri & Dayan, 2003). We note however that, although non-significant, also the two remaining species (*T. alba* and *T. longimembris*) showed a negative covariation between wing length and temperature. Remarkably, consistent clines in body shrinking in warm environments were observed in species living in different continents, showing a variable geographical range, and exploiting different habitats. For example, *T. tenebricosa-multipunctata* and *T. novaehollandiae* are taxa living almost exclusively in forested areas, while *T. furcata*, *T. javanica* and *T. capensis* are mainly found in open habitats. Taken together, these observations are in line with the prediction of Bergmann's rule, and strongly support the hypothesis that body size is, at least partly, convergently selected for body heat conservation depending on the thermal environment in this bird group.

The pattern of evolution of larger bodies in colder climates seems to be mainly driven by a latitudinal rather than an elevational variation in temperature. With the only exception of *T. javanica*, and in line with previous studies in birds (e.g. Olson et al., 2009) and mammals (e.g. Storz et al. 2001), the within-species effect sizes of the association between wing length and latitude are generally larger (or at most equivalent) than those between wing length and elevation. However, it is interesting to note that, although less intense, elevational gradients in body size seem to be as common as the latitudinal trends, thus driving measurable effects on birds' phenotype (Graves, 1991; Blackburn & Ruggiero 2001; Olson et al., 2009; but see also Freeman, 2017).

A convergent pattern of shrinking in body size at higher temperatures and lower latitudes was found among species showing a rather different latitudinal range (continental vs. multi-continental), average mean latitude (e.g. closer or farther from the Equator; see Figure 1), but also different range in temperatures (see Figure 2). However, the largest effects (especially for latitudes) are found in species living in a single continent (i.e. *T. capensis*, *T. novaehollandiae*, *T. tenebricosa-multipunctata*), rather than in those showing a wider distribution (i.e. *T. alba*, *T. furcata*, *T. longimembris*). A possible interpretation of this results is that, as suggested by previous studies (Ashton et al., 2002; Ashton, 2004; Meiri et al., 2007), in widely-distributed species the main drivers of body size variation may not act along a temperature (latitudinal, altitudinal or other geographical) gradient, but can be spatially affected by conditions present in different patches of their range. In addition, common patterns were found in all the continents (including Europe but only for minimum temperature), thus suggesting a rather generalized effect of temperature on body size in different part of the globe. In practice, the heat conservation mechanism seems to be valid for species occurring at different latitudes, and sampled over different latitudinal ranges, thus irrespectively of the distribution of the species under investigation.

However, some taxa, such as *T. longimembris* (and *T. alba* for mean temperature) in the present study (see also Ashton et al., 2002; Olson et al., 2009), seem to represent exceptions to such a general biogeographic rule. Why clear trends were not found in *T. longimembris* is a matter of speculation. A possible interpretation rests on the observation that this species can be nomadic in most of its distribution range and usually moves following the availability of resources (Clulow et al. 2011). Considering that sedentary birds have been shown to adhere more strictly to Bergmann's rule than migratory ones (Rensch 1936; Blacburn & Gaston, 1996; Ashton et al., 2002), it is not surprising that it is exactly this species not showing any clinal variation in body size. In addition, *T. longimembris* is mainly present on islands, and therefore body size can be primarily affected by islands size and peculiar climatic conditions in each island, thus potentially masking any general effect of temperature. In the case of *T. alba* distribution range corresponds with one of the most urbanized regions in the world (especially in Europe, where most of the data came from), which might have affected the expected association between temperature and body size. Indeed, in Europe most barn owls roost inside buildings where ambient temperature can be very different from external temperature.

Interestingly, body size is better predicted by variation in minimum, than maximum, annual temperature. In addition to the observation that the quadratic effect of temperature is never significant and considering that also spatial variation in bill length relative to body size is better explained by minimum than maximum temperatures (Romano et al., 2020a), this finding is compatible with the nocturnal habits of this bird genus, which is known to be sensitive to extreme winter cold (Altwegg et al., 2006). Indeed, nocturnal birds should not be particularly exposed to overheating because they are mainly active in the coldest part of the day. The opposite should be the case for species active during the daytime, for which proxies of body size have been observed to be mainly explained by summer temperatures (e.g. Andrew et al. 2018) or by both winter and summer climates (e.g. Fan et al. 2019).

On the other hand, we found little and less generalized support for the *resource availability* and *starvation resistance* hypotheses, although in some of the investigated species we could observe significant trends between body size and climatic proxies. However, we note that the proxies used for testing such hypotheses might not be as reliable predictors as the temperature is for the *heat conservation hypothesis*, thus potentially partly explaining why their association with wing length is less steep (or null) than that observed for temperature. However, the direction of the effect of evapotranspiration, a proxy of primary productivity, is variable, thus indicating that the abundance of resources may not play a major and general role in determining the evolution of body size in this bird group, as observed by previous intraspecific studies in other bird species (Murphy, 1985; Jones et al., 2005), even though it might be important in some species and regions (i.e. *T. alba* and *T. javanica*). The *Tyto* genus is composed of predator species only, hunting mainly small mammals but potentially shifting on other food sources when the prevalent prey is scarce (Taylor, 2003; Romano et al., in press). A possible interpretation for this result is that opportunistic predators might be less affected by the selective pressures imposed by peaks of food abundance than, for example, herbivore and insectivore species. In addition, it is possible that the *resource availability hypothesis* might be better supported when comparing different species or organism assemblages, as suggested by previous studies (Olson et al. 2009; Morales-Castilla et al., 2012), rather than in intraspecific analyses. The *starvation resistance hypothesis* is supported only in *T. tenebricosa-multipunctata*, despite generalized positive, but non-significant, trends emerged for all the species. It is therefore plausible that a strong seasonality in the availability of resources may marginally contribute to promote larger body sizes together with the major effect of conservation of body heat. Taken together with the observation that for all the species but *T. capensis* and *T. alba* the models including geographic predictors are the best supported models, these findings are compatible with previous results suggesting the possible concomitant action of different selective pressures, other than the major effect of temperature, driving body size along geographical gradients, at least for some species (see also James, 1970; Jones et al., 2005; Olson et al., 2009).

The present results can also help to better interpreting our recent findings on variation in bill length relative to body size in the common barn owl species complex (Romano et al., 2020a). According to Allen's rule (Allen, 1876), and compatibly with the role of the bill as a heat exchanging surface (e.g. Danner & Greenberg, 2015; Tattersal et al., 2017), we found that in *T. alba*, *T. furcata* and *T. javanica* relative bill length increases with temperature and decreases with latitude (and elevation but only in *T. furcata*). Such trends in bill length could have been therefore partly driven by a decrease in body size in warmer environments. In addition, we previously showed that in the barn owl species complex prey size tends to decrease at increasing latitude and decreasing temperature (Romano et al., 2020b), thus suggesting that body size might also be affected by the prey composition of the exploited habitats and/or that owls with different body size may rely on different hunting strategies. Future studies are needed to examine the relationships between body size, climate and diet.

Spatial and temporal patterns of variation in morphological and chromatic traits are attracting an increasing interest of scientists and public opinion because they can reflect generalized and predictable organismal responses to climate change. Indeed, growing evidence in endotherms has been provided about the association between temporal trends in morphology and the concomitant increase in temperature (e.g. Daufresne et al., 2009; Gardner et al., 2011;

Sheridan & Bickford, 2011; Yom-Tov & Geffen, 2011; Møller et al., 2018; Weeks et al., 2020). Unfortunately, with the present data we could not properly investigate the temporal variation in body size, possibly mirroring a response to the current global warming. However, the observation that body size convergently varies according to the prediction of Bergmann's rule in many species suggests that the changing thermal environments are probably forcing these birds to adapt to the new climatic conditions, possibly also via a shrinking in their body size. Further studies testing for among-year variation in body size and proportion in single locations are therefore needed to test for such a possibility in this bird family, but also in nocturnal raptors in general, where no information on potential effects of climate change on phenotype is available to date.

Declarations

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Conflicts of interest – None

Data availability – The dataset analysed in this study will be available via Dryad

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Data availability – The dataset analysed in this study will be available via Dryad after paper acceptance.

Biosketch - The main goal of the research group lead by Prof. Alexandre Roulin is to understand the role of natural and sexual selection in the evolution and maintenance of genetic and phenotypic variation in different morphological and chromatic traits and in their covariation by combining disciplines of evolutionary ecology, biogeography, behavioural ecology, genetics and population genetics/ genomics. Specific aims of our research are to determine the adaptive function of alternative phenotypes, identify how ecological, social and physiological factors influence and maintain inter-individual and inter-population variation in melanin-based coloration and other fitness-related traits.

Table legends

Table 1. Variation in wing length according to absolute latitude, elevation and island vs. mainland in the seven taxa of the *Tyto* genus. Hemisphere was also included as a predictor for the taxa which are present in both hemispheres. Elevation values were log-transformed to approximate a normal distribution (see main text).

Table 2. Variation in wing length according to mean annual temperature (a), actual evapotranspiration (b) or temperature annual range (c) in the seven taxa of the *Tyto* genus. In all the models, we also accounted whether an individual owl came from an island or mainland.

Table 1.

		Coefficient (SE)	t	P
Tyto alba				
	R^2	0.425		
	AIC	10067.57		
	Intercept	0.187 (0.177)		
	Island	-0.026 (0.044)	-0.59	0.56
	Absolute latitude	0.076 (0.123)	0.62	0.54
	Hemisphere	0.123 (0.104)	1.19	0.24
	Elevation	0.017 (0.032)	0.54	0.59
Tyto furcata				
	R^2	0.887		
	AIC	3134.478		
	Intercept	-0.121 (0.203)		
	Island	-0.077 (0.025)	-3.14	**0.002**
	Absolute latitude	0.279 (0.121)	2.30	**0.021**
	Hemisphere	--0.148 (0.071)	-2.10	**0.035**
	Elevation	0.045 (0.021)	2.13	**0.033**
Tyto javanica				
	R^2	0.819		
	AIC	1993.348		
	Intercept	-0.142 (0.288)		
	Island	-0.122 (0.056)	-2.19	**0.028**
	Absolute latitude	-0.234 (0.187)	-1.25	0.21
	Hemisphere	-0.355 (0.128)	-2.76	**0.006**
	Elevation	0.093 (0.027)	3.45	<**0.001**
Tyto capensis				
	R^2	0.339		
	AIC	483.6695		
	Intercept	-0.132 (0.182)		
	Absolute latitude	0.641 (0.188)	3.41	**<0.001**
	Elevation	0.201 (0.101)	2.00	**0.046**
Tyto longimembris				
	R^2	0.511		
	AIC	543.665		
	Intercept	-0.050 (0.078)		
	Island	0.198 (0.104)	1.91	0.06
	Absolute latitude	0.037 (0.094)	0.39	0.70
	Hemisphere	-0.271 (0.076)	-3.58	**0.003**
	Elevation	0.057 (0.081)	0.70	0.48
Tyto novaehollandiae				
	R^2	0.427		
	AIC	1039.539		
	Intercept	-0.050 (0.70)		
	Island	-0.128 (0.076)	-0.24	0.81
	Absolute latitude	0.559 (0.061)	9.08	**<0.001**
	Elevation	-0.100 (0.066)	-1.52	0.13
Tyto tenebricosa-Tyto multipunctata				
	R^2	0.598		
	AIC	220.1128		

Intercept	0.094 (0.144)		
Island	0.742 (0.201)	3.70	**<0.001**
Absolute latitude	1.108 (0.203)	5.47	**<0.001**
Elevation	0.105 (0.081)	1.30	0.19

Bold type indicates statistical significance

Table 2.

		Coefficient (SE)	t	P
a) Mean annual temperature				
Tyto alba				
	R^2	0.423		
	AIC	10064.2		
	Intercept	0.232 (0.198)		
	Island	-0.025 (0.044)	-0.57	0.57
	Temperature	-0.063 (0.062)	-1.00	0.32
Tyto furcata				
	R^2	0.886		
	AIC	3137.291		
	Intercept	-0.305 (0.305)		
	Island	-0.077 (0.025)	-3.13	**0.002**
	Temperature	-0.084 (0.034)	-2.48	**0.013**
Tyto javanica				
	R^2	0.817		
	AIC	2000.226		
	Intercept	0.025 (0.458)		
	Island	-0.138 (0.056)	-2.48	**0.013**
	Temperature	-0.212 (0.072)	-2.92	**0.003**
Tyto capensis				
	R^2	0.310		
	AIC	480.1616		
	Intercept	0.028 (0.300)		
	Temperature	-0.271 (0.081)	-3.36	**<0.001**
Tyto longimembris				
	R^2	0.349		
	AIC	547.993		
	Intercept	-0.417 (0.228)		
	Island	0.083 (0.129)	0.64	0.52
	Temperature	-0.012 (0.091)	-0.13	0.89
Tyto novaehollandiae				
	R^2	0.461		
	AIC	1045.597		
	Intercept	-0.029 (0.083)		
	Island	-0.103 (0.074)	-1.40	0.16
	Temperature	-0.590 (0.071)	-8.30	**<0.001**
Tyto tenebricosa-Tyto multipunctata				
	R^2	0.625		
	AIC	226.9553		
	Intercept	0.310 (0.480)		
	Island	0.137 (0.303)	0.45	0.65
	Temperature	-0.218 (0.111)	-1.97	**0.049**

		Coefficient (SE)	t	P
b) Actual evapotranspiration				
Tyto alba				
	R^2	0.424		
	AIC	10061.37		
	Intercept	0.178 (0.172)		
	Island	-0.025 (0.044)	-0.57	0.57
	Evapotranspiration	0.082 (0.041)	-1.97	**0.049**
Tyto furcata				
	R^2	0.886		
	AIC	3142.842		
	Intercept	0.271 (0.335)		
	Island	-0.078 (0.025)	-3.18	**0.001**
	Evapotranspiration	-0.026 (0.035)	0.75	0.45
Tyto javanica				
	R^2	0.817		
	AIC	2003.90		
	Intercept	-0.071 (0.417)		
	Island	-0.132 (0.056)	-2.35	**0.019**
	Evapotranspiration	0.145 (0.066)	2.20	**0.028**
Tyto capensis				
	R^2	0.332		
	AIC	488.9605		
	Intercept	-0.168 (0.285)		
	Evapotranspiration	-0.196 (0.186)	-1.05	0.29
Tyto longimembris				
	R^2	0.347		
	AIC	547.9893		
	Intercept	-0.412 (0.229)		
	Island	0.077 (0.135)	0.57	0.57
	Evapotranspiration	0.016 (0.108)	0.15	0.88
Tyto novaehollandiae				
	R^2	0.405		
	AIC	1055.725		
	Intercept	-0.672 (0.444)		
	Island	-0.093 (0.135)	-0.69	0.49
	Evapotranspiration	-0.144 (0.110)	-1.31	0.19
Tyto tenebricosa-Tyto multipunctata				
	R^2	0.648		
	AIC	229.7851		
	Intercept	0.417 (0.683)		
	Island	0.055 (0.386)	0.14	0.89
	Evapotranspiration	0.127 (0.144)	0.89	0.38

		Coefficient (SE)	t	P
c) Temperature annual range				
Tyto alba				
	R^2	0.425		
	AIC	10062.04		
	Intercept	0.195 (0.169)		
	Island	-0.09 (0.045)	-0.21	0.84
	Temperature annual range	0.088 (0.049)	1.79	0.07
Tyto furcata				
	R^2	0.887		
	AIC	3141.825		
	Intercept	-0.235 (0.303)		
	Island	-0.073 (0.025)	-2.96	**0.003**
	Temperature annual range	0.077 (0.061)	1.26	0.21
Tyto javanica				
	R^2	0.817		
	AIC	2008.374		
	Intercept	0.007 (0.426)		
	Island	-0.125 (0.058)	-2.7	**0.030**
	Temperature annual range	0.046 (0.079)	0.57	0.57
Tyto capensis				
	R^2	0.341		
	AIC	487.7219		
	Intercept	-0.082 (0.345)		
	Temperature annual range	0.257 (0.170)	1.51	0.13
Tyto longimembris				
	R^2	0.348		
	AIC	547.9736		
	Intercept	-0.414 (0.227)		
	Island	0.099 (0.155)	0.64	0.52
	Temperature annual range	0.026 (0.136)	0.19	0.85
Tyto novaehollandiae				
	R^2	0.397		
	AIC	1057.347		
	Intercept	-0.727 (0.696)		
	Island	-0.097 (0.141)	-0.69	0.49
	Temperature annual range	0.007 (0.080)	0.091	0.93
Tyto tenebricosa-Tyto multipunctata				
	R^2	0.641		
	AIC	224.0955		
	Intercept	0.420 (0.501)		
	Island	0.443 (0.311)	1.43	0.15
	Temperature annual range	0.495 (0.189)	2.62	**0.009**

Bold type indicates statistical significance

Figure legends

Figure 1. Recovery locations of all the specimens of the seven taxa of the genus *Tyto* included in the analyses.

Figure 2. Relationship between mean annual temperature and wing length in the seven taxa of the genus *Tyto* included in the analyses. Regression lines and 95% confidence intervals (grey bands) from the models reported in Table 2 are shown. Black dots represent raw data.

Figure 1

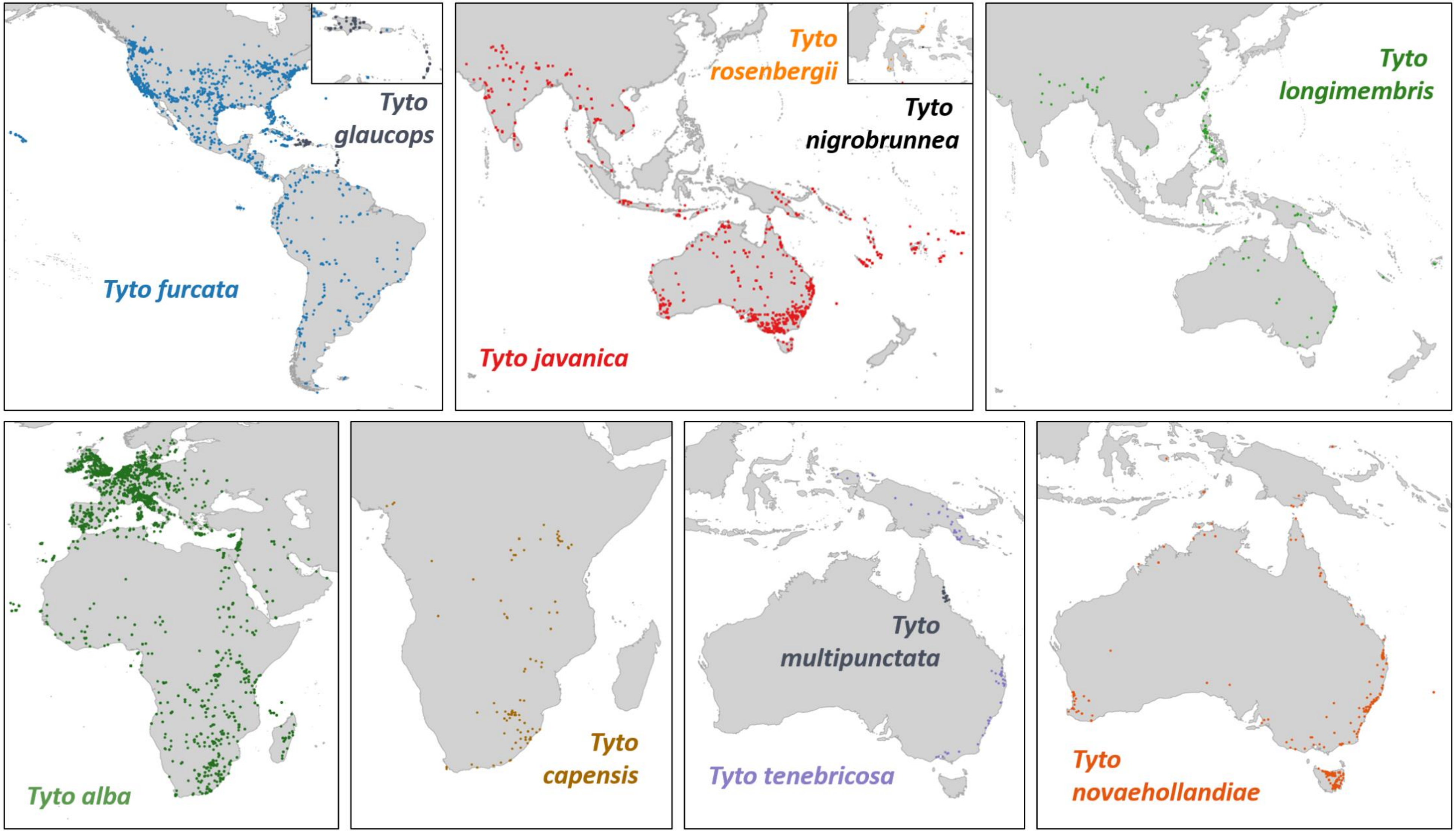
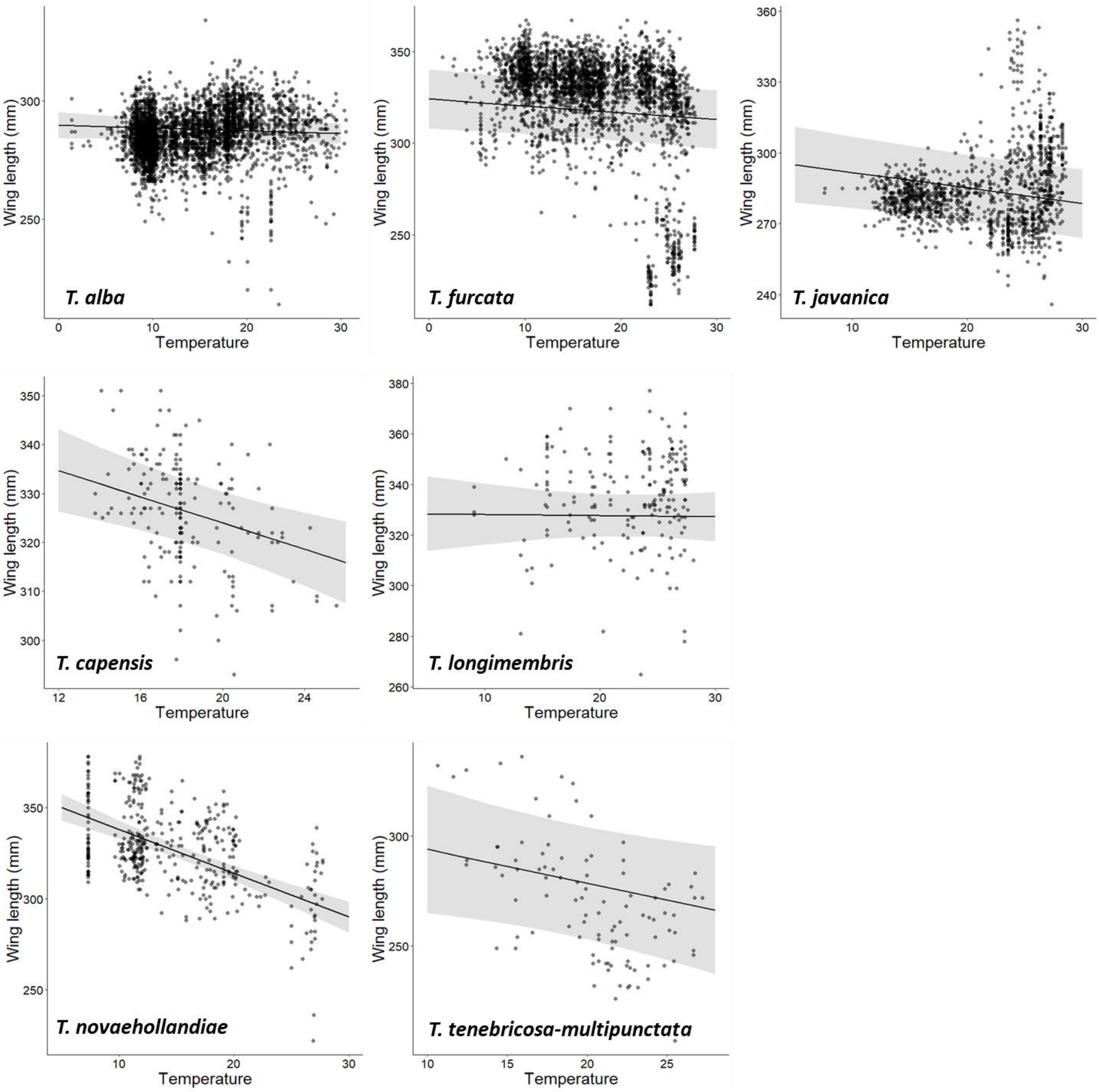

Tyto glaucops
Tyto furcata
Tyto rosenbergii
Tyto nigrobrunnea
Tyto javanica
Tyto longimembris
Tyto alba
Tyto capensis
Tyto multipunctata
Tyto tenebricosa
Tyto novaehollandiae

Figure 2.



T. alba
T. furcata
T. javanica
T. capensis
T. longimembris
T. novaehollandiae
T. tenebricosa-multipunctata
Wing length (mm)
Temperature

Table S1. Variation in wing length according to minimum and maximum annual temperature in the seven taxa of the *Tyto* genus. In all the models, we also accounted whether an individual owl came from an island or mainland.

		Coefficient (SE)	t	P
Tyto alba				
	R^2	0.424		
	AIC	10063.1		
	Intercept	0.254 (0.187)		
	Island	-0.011 (0.045)	-0.24	0.81
	Minimum temperature	-0.138 (0.068)	-2.02	**0.043**
	Maximum temperature	0.053 (0.062)	0.86	0.39
Tyto furcata				
	R^2	0.886		
	AIC	3138.064		
	Intercept	-0.268 (0.283)		
	Island	-0.073 (0.025)	-2.95	**0.003**
	Minimum temperature	-0.139 (0.066)	-2.11	**0.035**
	Maximum temperature	-0.001 (0.033)	-0.04	0.97
Tyto javanica				
	R^2	0.817		
	AIC	2001.206		
	Intercept	0.041 (0.463)		
	Island	-0.133 (0.057)	-2.33	**0.020**
	Minimum temperature	-0.193 (0.097)	-1.99	**0.047**
	Maximum temperature	-0.080 (0.059)	-1.35	0.18
Tyto capensis				
	R^2	0.318		
	AIC	482.3709		
	Intercept	0.035 (0.315)		
	Minimum temperature	-0.309 (0.119)	-2.61	**0.009**
	Maximum temperature	-0.130 (0.106)	-1.22	0.22
Tyto longimembris				
	R^2	0.348		
	AIC	549.9736		
	Intercept	0.414 (0.227)		
	Island	0.099 (0.156)	0.64	0.53
	Minimum temperature	-0.028 (0.151)	-0.19	0.85
	Maximum temperature	0.018 (0.116)	0.16	0.87
Tyto novaehollandiae				
	R^2	0.461		
	AIC	1048.125		
	Intercept	-0.031 (0.084)		
	Island	-0.142 (0.101)	-1.41	0.16
	Minimum temperature	-0.235 (0.114)	-2.05	**0.040**
	Maximum temperature	-0.405 (0.152)	-2.67	**0.008**
Tyto tenebricosa-Tyto multipunctata				
	R^2	0.635		
	AIC	225.6452		

Intercept	0.382 (0.472)		
Island	0.407 (0.304)	1.34	0.18
Minimum temperature	-0.597 (0.254)	-2.35	**0.019**
Maximum temperature	0.285 (0.212)	1.34	0.18

Bold type indicates statistical significance

Figure S1. Relationship between mean annual actual evapotranspiration and wing length in the seven taxa of the genus *Tyto* included in the analyses. Regression lines and 95% confidence intervals (grey bands) from the models reported in Table 2 are shown. Black dots represent raw data.

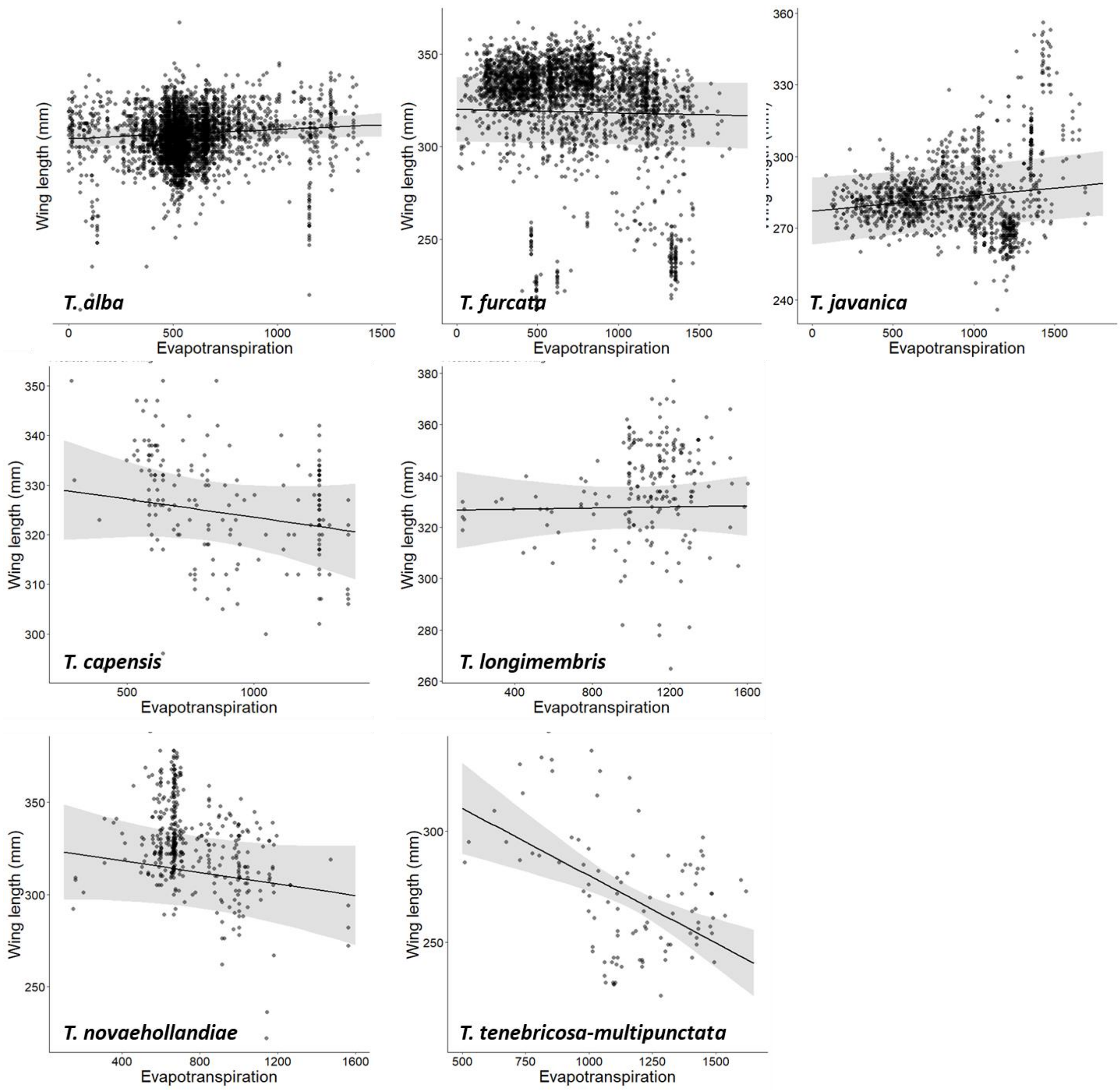


Figure S2. Relationship between temperature annual range and wing length in the seven taxa of the genus *Tyto* included in the analyses. Regression lines and 95% confidence intervals (grey bands) from the models reported in Table 2 are shown. Black dots represent raw data.