

EVOLUTION OF MOULTING STRATEGIES AND ALTITUDINAL MIGRATION OF
PASSERINES

by

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ABSTRACT

Each year, migratory birds need to undertake three main energetically costly events: breeding, migration, and moulting. While most species separate these three events during the annual cycle and share the same moulting and migration strategies, some species have evolved a variety of different moulting and migratory strategies. The goal of my thesis was to understand the evolution of these particular moulting and migratory strategies and which environmental factors or life history characteristics may have driven their evolution. Particularly, I was interested in the evolution of moult-migration, winter moults, and altitudinal migration in passerines (i.e., perching birds). To do so, I used phylogenetic analyses to correct for non-independence among species. My results indicated that arid breeding grounds were associated with moult-migration in North American passerines; the lack of resources during late summer appeared to force birds to migrate to more productive moulting grounds such as the Mexican monsoon region. I also found an association between the conditions on the wintering grounds and the evolution of winter moults for North American and European passerines. Specifically, longer day lengths on the overwintering grounds were associated with a single moult on the wintering grounds and also the presence of a second moult. Overwintering in open habitats was also associated with the presence of a second, winter moult for European passerines; birds experiencing longer day lengths and open habitats are subject to higher UV exposure which increases feather wear and may force birds to moult some feathers a second time. Completely moulting twice during the annual cycle was associated with high primary productivity on the wintering grounds for European passerines. Finally, I examined all passerines around the globe and found that altitudinal migration was associated with diet, but the nature of the relationship varied within regions. In North America, species with a plant and fruit diet or omnivorous diet were more likely to evolve altitudinal migration; in Europe and north Asia, omnivorous species were more likely to be altitudinal migrants. All these results indicate the importance of environmental conditions and life history characteristics in the evolution of moult and migration strategies.

Keywords: Phylogenetic analysis, Moult-migration, Altitudinal migration, Winter moult, Prealternate moult.

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CHAPTER 1: INTRODUCTION

Long-distance movements are common in the life history of many bird species, with migrations often spanning thousands of kilometres, crossing oceans and continents. Many birds migrate twice a year to move from their temperate breeding grounds, where they reproduce, to their tropical wintering grounds for the non-breeding season. Most species will migrate by changing latitude (e.g., northern hemisphere to southern hemisphere and vice-versa), but some species will also move upslope or downslope in a process termed altitudinal migration. Migration is time-consuming and requires massive amounts of energy (Alerstam 2011); as a consequence, the timing and pattern of migration a bird undergoes influences all aspects of its annual cycle, including breeding and moulting (i.e., the replacement of old feathers for new ones; Humphrey and Parkes 1959; Svensson and Hedenström 1998).

Generally, passerines (perching birds) moult on their breeding grounds after reproduction and only moult once during the year (Humphrey and Parkes 1959). However, migration imposes a constraint on the schedule of moult during the annual cycle, which results in the evolution of various moult strategies in migrant passerines. A moult strategy is defined by the location, time, and number of feathers replaced (Jenni and Winkler 2020). Passerines can undergo a single moult (called a prebasic moult) during the annual cycle or moult partially or completely a second time (a prealternate moult) (Humphrey and Parkes 1959; Jenni and Winkler 2020). Having two complete moults (that is having a biannual moult) is rare among North American passerines, but more common among European species. The location of the moult can vary from the breeding grounds to the wintering grounds or there can be an overlap between moult and migration which is termed moult-migration (Tonra and Reudink 2018).

Moult-migration is a moulting strategy that occurs in a range of unrelated passerines in North-America, including Bullock's Orioles (*Icterus bullockii*, Pillar et al. 2016), Western Kingbirds (*Tyrannus verticalis*, Barry et al. 2009), and Western Tanagers (*Piranga ludoviciana*, Butler et al. 2002). These species interrupt their fall migration at a particular location, termed a stopover site, to replace their feathers (Tonra and Reudink 2018). An

30 important stopover site is the Mexican monsoon region located in Northwestern Mexico and
 31 Southwestern USA. At the end of the summer, during the monsoon rains, an abundance of
 32 resources essential for the process of moult is produced in this region (Figure 1; Leu and
 33 Thompson 2002; Rohwer et al. 2005). This explosion of resources arrives at the same time as
 34 birds migrate over the area, which thus, draws some species to interrupt their fall migration
 35 to take advantage of this abundance.



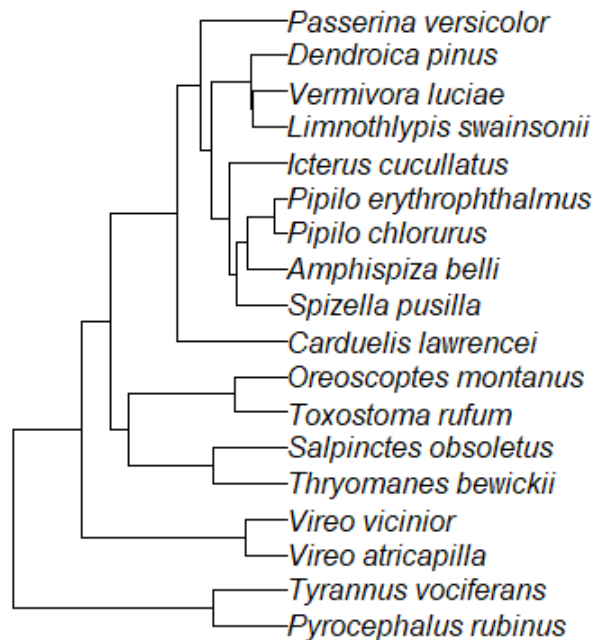
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37 **Figure 1.1.** Explosion of productivity in the Mexican monsoon region at the end of the
 38 summer (David K. Adams and Arturo Quintanar, Hidrología y meteorología, CCA, UNAM).

39 In addition to the various moult strategies birds display, there is also a wide range of
 40 migration strategies, including altitudinal migration. Altitudinal migration is defined as
 41 seasonal movements from lower to higher elevations and vice versa (Hayes 1995; Mackas et
 42 al 2010; Barçante et al. 2017). Worldwide, 830 passerines across 77 families are considered
 43 altitudinal migrants. Because altitudinal migration has been less studied than latitudinal
 44 migration (South to North movements), the drivers behind the evolution of this strategy

45 remain unclear. Research has suggested links between altitudinal migration and a reduction
46 in the risk of predation (Boyle 2008a), avoidance of harsh climatic conditions (Hahn et al.
47 2004; Boyle 2008b; Boyle et al. 2010), and tracking of food resources (Levey 1988; Loiselle
48 and Blake 1991; Solorzano et al. 2000; Kimura et al 2001; Chaves-Campo 2004).

49 While studies have looked at the drivers of the different moult and migration
50 strategies, most have considered only a few species or/and did not take into account the
51 phylogenetic relationship among species (Felsenstein 1985; Harvey and Pagel 1991).
52 Phylogenetic relationships represent how related species are to each other. These
53 relationships can be visualized using phylogenetic trees or cladograms, in which each branch
54 represents a species or group of species and the length of the branches indicates how distant
55 the species are from each other in term of their evolutionary relationships (Figure 2). When
56 studying evolutionary phenomena, it is important to use phylogenetic analysis to correct for
57 non-independence among species (Felsenstein 1985; Harvey and Pagel 1991; Ives and Zhu
58 2006). Phylogenetically-controlled analyses are statistical tests that incorporate the addition
59 of a phylogeny to take into account the relationships among species. Without the addition of
60 a phylogeny, false correlations are common. This is because closely related species often
61 express the same traits, not because they evolved these particular traits independently, but
62 because they share common ancestors in which these traits were evident. Phylogenetic
63 analyses correct for this problem by, for example, considering two sister species with the
64 common trait as only one evolutionary event instead of two.



65

66 **Figure 1.2.** Example of a phylogeny represented by a phylogenetic tree. The tips of the
 67 branches represent a taxon (species or group of species) and the length of the branches
 68 indicates the time since the taxa diverged.

69 The purpose of my research is to answer large-scale evolutionary questions about the
 70 evolution of moulting strategies in North American and European passerines and, also, about
 71 the evolution of altitudinal migration for passerines worldwide. I will do so using
 72 phylogenetic analyses to correct for the non-independence among species. My goal is to
 73 identify environmental factors and life history characteristics that could be potential drivers
 74 of the evolution of moult-migration in North American passerines, winter moults in North
 75 American and European passerines, and altitudinal migration in passerines worldwide.

76 This thesis is divided into three research chapters that each focus on one particular
 77 question; it finishes with a conclusion chapter. Chapter 2 focuses on the drivers of the
 78 evolution of moult-migration in North American migrant passerines. Chapter 3 compares the
 79 factors that influence the evolution of winter moults in Nearctic and Western Palearctic
 80 migrant passerines and chapter 4 examines the potential drivers behind the evolution of
 81 altitudinal migration in passerines globally.

82 Chapter 2 was published in *Biology Letters* (Pageau et al. 2020a) and Chapter 4 was
83 published in *Ecology & Evolution* (Pageau et al. 2020b). Chapter 3 is currently in review at
84 *Ecography*.

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179 **CHAPTER 2: EVOLUTION OF MOULT-MIGRATION IS DIRECTLY LINKED TO**
180 **ARIDITY OF THE BREEDING GROUNDS IN NORTH AMERICAN PASSERINES**

181 Published in Biology Letters

182 **ABSTRACT**

183 To avoid energy allocation conflicts, birds generally separate breeding, migration,
184 and moult during the annual cycle. North American passerines typically moult on the
185 breeding grounds prior to fall migration. However, some have evolved a moult-migration
186 strategy in which they delay moult until stopping over during fall migration. Rohwer et al.
187 (2005) proposed the “push-pull hypothesis” as an explanation for the evolution of this moult
188 strategy, but it has not been empirically tested. Poor conditions on the breeding grounds at
189 the end of the summer would push birds to depart prior to moult, while productive stopover
190 locations would pull them. We tested for a relationship between moult-migration and
191 breeding grounds aridity as measured by the normalized difference vegetation index (NDVI).
192 Our results strongly support the “push” aspect of the push-pull hypothesis and indicate that
193 arid breeding grounds, primarily in western North America, would drive species to evolve
194 stopover moult-migration, although this relationship may depend upon migration distance.

195

196 **INTRODUCTION**

197 Feathers are unique to birds and are critical to nearly every aspect of their biology,
198 including flight, thermoregulation, and visual communication (Gill 1994). Each year, birds
199 must exchange old feathers for fresh ones by moulting (Humphrey and Parkes 1959;
200 Svensson and Hedenström 1999). An energetically expensive stage of the annual cycle (Dietz
201 et al. 1992; Murphy and King 1992; Lindström et al. 1993; Howell 2010; Hoyer and
202 Buttermer 2011), moulting requires specific resources to produce high-quality feathers.
203 Hence, the timing and location of moult are crucial for the production of feathers of sufficient
204 quality to maximize lifetime reproductive success (Echeverry-Galvis and Hau 2013). To
205 avoid energy allocation conflicts, birds generally separate the most energetically expensive
206 life history events during the annual cycle: breeding, migration, and moult (Wingfield 2008).
207 Most migratory passerines complete their moult on the breeding grounds prior to fall

208 migration. However, some have evolved a moult-migration strategy, the “temporal overlap in
209 the moult and migration life history stages” (Tonra and Reudink 2018).

210 Moving to a stopover location i.e., a rest/refueling site during migration (Newton
211 2008), to moult (stopover moult-migration; Tonra and Reudink 2018) or moulting during
212 migration (continuous moult-migration; Tonra and Reudink 2018) must confer benefits that
213 outweigh the costs of overlapping these two energetically demanding life history stages. One
214 advantage to continuous moult-migration could be reducing the overall time utilized for these
215 events, thus advancing arrival date at stationary non-breeding grounds, which might provide
216 various advantages (see below). For stopover moult-migration, an advantage might be the
217 ability to acquire high quality resources to support moulting. For example, various species
218 breeding in western North America moult in the monsoon region of northwestern Mexico
219 and southwestern USA (Rohwer et al. 2005; Pyle et al. 2009). Here, the late-summer
220 monsoon rains result in an explosion of productivity that may “pull” species to this area to
221 take advantage of abundant resources (Rohwer and Manning 1990; Rohwer et al. 2005).

222 While the richness of the Mexican monsoon region may “pull” moult-migrants to
223 stopover, other factors may also “push” them to depart prior to moult, including aridity of the
224 breeding grounds at the end of the summer or a time constraint at high latitudes. The
225 combination of good conditions at stopover locations with unfavorable conditions on the
226 breeding grounds during the post-breeding period forms the push-pull hypothesis. This
227 hypothesis has often been proposed as an explanation for the evolution of stopover moult-
228 migration in the Mexican monsoon region (Rohwer et al. 2005; Barry et al. 2009; Bridge et
229 al. 2016), but has not yet been empirically tested.

230 Several drivers of moult-migration evolution have been hypothesized, such as
231 migration distance, aridity of the breeding grounds during the post-breeding period, winter
232 territoriality, length of the breeding season, and number of broods produced during the
233 breeding season. Long migration distances and a long breeding season, especially if raising
234 multiple broods, may reduce the time available between the end of breeding and start of
235 migration and not allow for the replacement of all feathers (Kjellén 1994; Lesley et al. 1996;
236 Hall and Tullberg 2004; Benson and Winker 2015). Arid breeding grounds could select for
237 moult-migration because the lack of resources at the end of summer in western North

238 America limits the ability to grow feathers of sufficient quality (Young 1991; Rohwer et al.
239 2005). Finally, moult-migration might be favoured in species that defend non-breeding
240 territories because it would allow earlier arrival at the non-breeding grounds, and thus the
241 acquisition of higher quality territories (Lindström et al. 1993; Pérez and Hobson 2006).

242 Revealing the mechanisms responsible for the evolution of overlapping life history
243 stages is critical to understanding the dynamics of migratory bird populations and how they
244 are limited. Migration places enormous time constraints on avian life histories, the
245 organization of which is shaped by both biotic and abiotic factors (Wingfield 2008).
246 Environmental changes, including land use and global climate alterations, are shifting the
247 availability of resources both spatially and temporally, potentially altering the playing field
248 of selection (e.g., Siepielski et al. 2017). Understanding the factors that drive the
249 organization of annual cycles will help us predict the resilience of species to environmental
250 change, as well as identify species in need of proactive management (Marra et al. 2015).

251 Using phylogenetic comparative analyses, we examined the hypothesis that
252 unfavorable (dry) breeding grounds conditions during the post-breeding period act as a
253 “push” for 1) moult-migration in North American passerines, and 2) explicitly the evolution
254 of stopover moult-migration in the Mexican monsoon region. We used the normalized
255 difference vegetation index (NDVI) as a measure of the aridity of breeding grounds. We also
256 tested other factors that have been proposed to influence the evolution of moult migration:
257 migration distance, winter territoriality, and number of broods.

258

259 **METHODS**

260 *Data Collection*

261 We collected data for 200 species and 5 subspecies of migratory passerines breeding
262 in Canada and/or the USA. Three species (*Vireo gilvus*, *Haemorhous purpureus*, and
263 *Passerina ciris*) were divided into their Eastern and Western subspecies or populations,
264 which differ in moult strategy, for a total of 208 taxa. We classified species with respect to
265 where they undergo prebasic moult (i.e., complete moult resulting in the basic plumage
266 (Humphrey and Parkes 1959): breeding, wintering grounds or during migration. We followed

267 Tonra and Reudink's (2018) classification to specify which category of moult-migration
268 (stopover, continuous, or suspended) the species conformed to. To determine prebasic
269 moulting strategy, we used descriptions of moulting from Birds of North America species
270 accounts (The Birds of North America 2019), Pyle (Pyle 1997), and the literature (Voelker
271 and Rohwer 1998; Butler et al. 2002; Rohwer et al. 2005; Butler et al. 2006; Pyle et al. 2009;
272 Jahn et al. 2013; Pyle et al. 2018). When variation in moulting strategy among individuals of
273 the same species was encountered, we classified that species as a moult-migrant. Altitudinal
274 migrants (6 species) were categorized as moulting on their breeding grounds.

275 *Potential Drivers of Moult-Migration*

276 Migration distance was approximated as the distance (Mm) from the centroid of the
277 breeding distribution to the centroid of the non-breeding distribution using the package
278 Geosphere (Hijmans 2019) in R (R Core Team 2019). Centroid values were calculated in
279 decimal degrees using polygon maps provided by Birdlife International (BirdLife
280 International 2018) in ArcMap. For 76 species, the polygon maps were absent for either
281 breeding or non-breeding distributions and the centroid values were calculated by creating
282 polygons in Google Earth pro using template maps from IUCN (2019) and processing the
283 polygons in Earth Point (2020). For 15 species, the breeding or non-breeding distribution
284 maps were not available. Instead, we used the resident distribution maps to calculate the
285 migration distance between breeding and resident grounds or non-breeding and resident
286 grounds.

287 Distribution maps from Birdlife International (2018) were used in the calculation of
288 normalized difference vegetation index (NDVI). NDVI is a measure of live green vegetation
289 and was used to indicate the aridity of the breeding grounds during the post-breeding period
290 in North America. Data were available from the Application for Extracting and Exploring
291 Analysis Ready Samples (AppEEARS Team 2019). We extracted the NDVI values from July
292 1 to August 31 from 2000 to 2019 using the "Area Sample" function, chose the product
293 MOD13A3.006 (Didan 2015), selected "Native projection", and calculated the mean value
294 for each species. For 72 species, the distribution maps were missing or not useable in
295 AppEEARS. Instead, we created distribution maps as polygons using template maps from

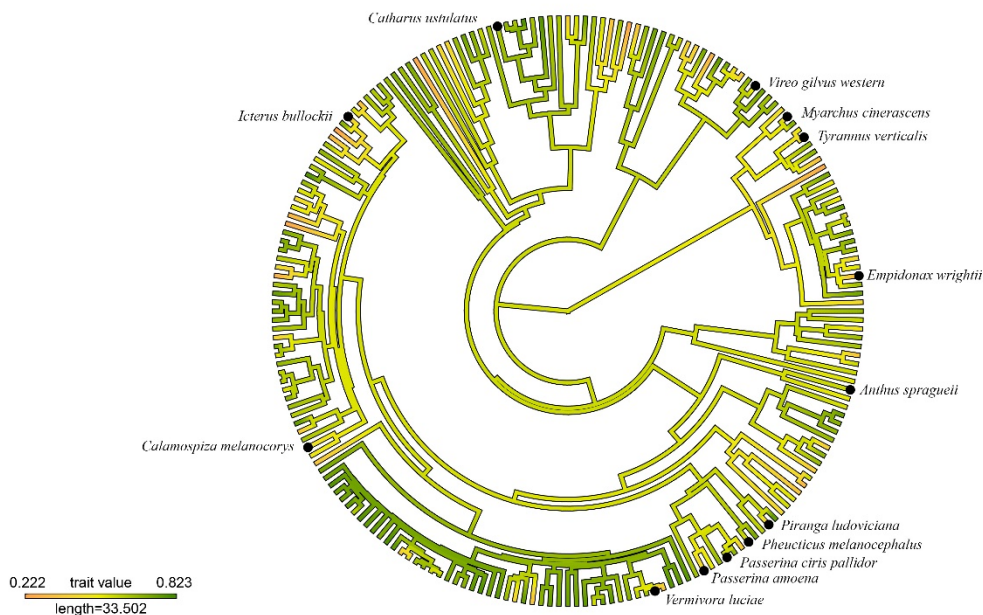
296 IUCN (2019). Finally, five species had overlapping resident and breeding distributions in
297 IUCN (2019). For these, we used NDVI from the map showing their resident distribution.

298 Winter territoriality category (yes or no) was taken from Birds of North America
299 (2019). In cases where winter territoriality was not definitive, or territoriality was mentioned
300 only in the section on breeding, the species were considered non-territorial during the winter.

301 Data on the number of broods were retrieved from Birds of North America (2019).
302 This predictor was categorical: one or multiple broods. We considered the most widespread
303 behavior to be typical for the number of broods. Datum for *Dendroica coronata auduboni*
304 was gathered from the Handbook of the Birds of the World (del Hoyo et al. 2019) because
305 number of brood datum was missing in Birds of North America (2019). The two obligate
306 brood parasites were assigned to the one brood category since they provide minimal parental
307 care.

308 *Phylogeny*

309 Using BirdTree.org (Jetz et al. 2012), we downloaded 1000 possible trees of a
310 phylogeny subset containing our 200 species of passerines from “Hackett All Species: a set
311 of 10000 trees with 9993 OTUs each” (Hackett et al. 2008). Using TreeAnnotator V.1.10.4
312 (Rambaut and Drummond 2018), we then created a maximum clade credibility tree with our
313 1000 trees using 1% burn-in (as states) and mean heights for node heights. We added the 8
314 subspecies in R (R Core Team 2019) to obtain a maximum clade credibility tree of 208
315 species and subspecies, which we used for all our analysis. The visual representation of our
316 phylogeny (Figure 2.1) was created using the phytools package of R (Revell 2012).



317

318 **Figure 2.1.** Phylogeny of the 208 species of North American migrant passerines. The colour
 319 of the branches represents the average NDVI of the breeding grounds in July and August for
 320 each passerine: green indicates high NDVI values and tan low values. The black circles
 321 indicate species that are stopover moulting-migrants; these are labelled with the scientific name
 322 of these species.

323 *Statistical Analysis*

324 We used phylogenetically-controlled analysis to investigate factors associated with
 325 the evolution of moulting-migration (including stopover, suspended, and continuous moulting; 45
 326 species) and specifically the stopover moulting-migration strategy (13 species) for which the
 327 push-pull hypothesis was originally devised. Note, however, that we could only test the
 328 “push” aspect of the hypothesis because moulting distributions are unavailable. In both
 329 (stopover or moulting-migration), the response variables were binary, with 1 indicating presence
 330 of stopover or moulting-migration and 0 indicating absence. We then used phylogenetic logistic
 331 linear models to test the predictors by creating a full model that included all explanatory
 332 variables (NDVI, migration distance, number of broods, and winter territoriality) and
 333 sequentially eliminated non-significant variables ($p > 0.05$) to arrive at a final best fit model.
 334 No explanatory variables were highly correlated (all $r < 0.31$). Analyses were conducted in R
 335 (R Core Team 2019) using the package phyloglm (Ho and Ane 2014). The “logistic_MPLE”
 336 method was applied with a “btol” of 10, a “log.alpha.bound” of 10, and no bootstrap.

337

338 RESULTS

339 When we examined the factors associated with moult-migration, both NDVI ($z = -$
 340 2.72 , $p = 0.006$) and migration distance ($z = 2.68$, $p = 0.007$) were retained in the final model,
 341 indicating that moult-migrants were more likely to migrate longer distances and have
 342 breeding ranges that are drier in the post-breeding period than non-moult migrants. Next, we
 343 specifically examined the stopover moult migration strategy. In this case, only NDVI of the
 344 breeding range was included in the final model and was strongly negatively associated with
 345 stopover ($z = -3.49$, $p = 0.0005$), indicating that the breeding areas of stopover moult-
 346 migrants were drier during the post-breeding period than those of non moult-migrants (Table
 347 2.1).

348 **Table 2.1.** Predictors of stopover and moult-migration included in the best model of the
 349 phylogenetic logistic regression following a stepwise regression (backward elimination).
 350 Stopover = stopover moult-migration strategy only ($n=13$ species), Moult-migration =
 351 stopover, continuous and suspended moult-migration combined ($n = 45$ species).

	Coefficient	Estimate	Std. Error	z-value	p
Stopover	Intercept	0.70	0.88	0.79	0.43
	NDVI	-6.31	1.81	-3.49	0.0005
Moult-migration	Intercept	-0.17	0.60	-0.29	0.77
	Migration distance	0.26	0.096	2.68	0.007
	NDVI	-2.93	1.08	-2.72	0.006

352

353 DISCUSSION

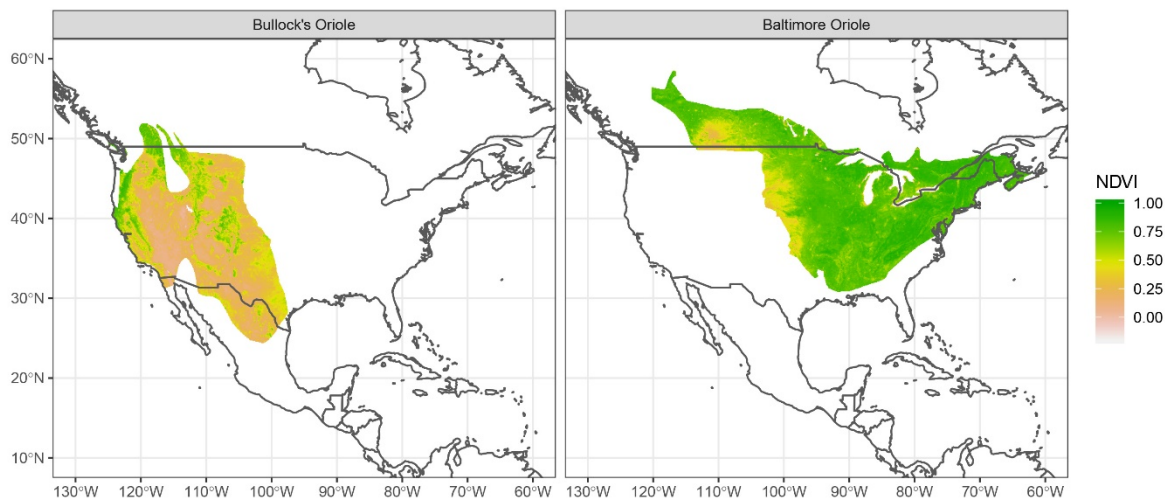
354 We tested four hypotheses (aridity of the breeding grounds during the post-breeding
 355 period, migration distance, presence or absence of winter territoriality, and number of
 356 broods) that have been proposed to explain the evolution of moult-migration in North
 357 American passerines. Of the four factors, our analyses suggested that NDVI was
 358 evolutionarily associated with moult-migration, in particular the strategy that involves a
 359 stopover in the Mexican monsoon region during migration. Taxa with breeding grounds that
 360 are dry and unproductive during the post-breeding period (indicated by low NDVI values)
 361 showed a stopover moult-migration strategy much more often than expected by chance alone.
 362 In addition, longer migration distances were also evolutionarily associated with moult-

363 migration when suspended, continuous, and stopover strategies are combined in one
364 category.

365 Aridity has long been proposed as a driver of moult-migration; however, explicit tests
366 of this hypothesis have been lacking. Rohwer et al. (2005) and Young (1991), raised the idea
367 that arid breeding grounds may offer insufficient resources at the end of the summer to grow
368 high-quality feathers, which are essential for flight performance during fall migration.
369 Substantial energy is required to synthesize new feathers (Dietz et al. 1992; Murphy and
370 King 1992; Lindström et al. 1993), thus having an abundance of high-quality resources
371 during moulting is critical. Limitation of resources at the end of the summer would act as a
372 “push” towards moult-migration in North America, particularly in the West, where lowlands
373 become dry and unproductive (Figure 2.2; Young 1991) at this time. The Mexican monsoon
374 region in northwestern Mexico and southwestern USA is an important stopover location to
375 undergo moult for migrant passerines (Leu and Thompson 2002) such as *Icterus bullockii*
376 (Pillar et al. 2016), *Tyrannus verticalis* (Barry et al. 2009), and *Piranga ludoviciana* (Butler
377 et al. 2002). Monsoon rains in this region in July and August result in an explosion of
378 resources available for migrant passerines on their way to the non-breeding grounds (Comrie
379 and Glenn 1998). An attraction to the Mexican monsoon region, combined with the aridity of
380 the breeding grounds at the end of the summer, likely drove the evolution of some western
381 North American migrant passerines toward stopover moult-migration.

382

383



384

385 **Figure 2.2.** Distribution maps representing NDVI of the breeding grounds (July 1st to
 386 August 31) of two North American passerines. Higher values indicate a greater abundance of
 387 live green vegetation. *Icterus galbula* (Baltimore Orioles) moult on their breeding grounds
 388 and their NDVI average is 0.83. *I. bullockii* (Bullocks Orioles) are stopover moult-migrants
 389 and their NDVI average is 0.35.

390 For the alternative factors tested, only migration distance was associated with moult-
 391 migration; winter territoriality and number of broods were not present in the best models. As
 392 expected, longer migration distances were associated with moult-migration: by imposing a
 393 time constraint, they would force moult outside of the breeding grounds (Hall and Tullberg
 394 2004; Benson and Winker 2015). This result is in accordance with previous European studies
 395 on Sylviidae (Hall and Tullberg 2004) and Western Palearctic passerines (Kiat et al. 2019)
 396 that indicated longer migration distance as a driver of moulting strategies differing from the
 397 ancestral state (moult on the breeding grounds) (Svensson and Hedenström 1998). A time
 398 constraint was also the reason why number of broods was proposed as a predictor, but our
 399 results suggest this variable was not important in the evolution of moult-migration. Winter
 400 territoriality was hypothesized as driving moult-migration and winter moult by Pérez &
 401 Hobson (2006) and Lindström et al. (1993), but our results concur with Rohwer et al. (2005),
 402 who did not support the winter territoriality hypothesis.

403 Our research examined 208 North American migrant passerines and classified each
 404 species as moult-migrant or not. While some species have extensive data and were easy to fit
 405 into a category (e.g., *I. bullockii*; Pillar et al. 2016), those exhibiting intra-specific variation
 406 in moulting strategy were more challenging. In addition, Pyle et al. (2018) described a wide

407 variety of post-breeding dispersal movements for moulting in many passerines. These
408 dispersal movements might be a type of moult-migration; however, we took a conservative
409 approach in our analysis and did not account for these movements since they do not fit the
410 definition of moult-migration provided by Tonra and Reudink (2018). Intra-specific variation
411 also exists for the explanatory variables (migration distance, winter territoriality, number of
412 broods): thus, these categorizations at the species level are purposely rough in an effort to
413 describe broad scale taxonomic and geographic patterns, and a more detailed and nuanced
414 study that accounted for that variation at the individual level would be useful for future
415 research.

416 Our results strongly support the “push” aspect of the push-pull hypothesis proposed
417 by Rohwer et al. (2005); arid breeding grounds during the post-breeding period “push” some
418 migrant passerines towards a stopover moult-migration strategy that capitalizes on the
419 abundant resources available in the Mexican monsoon region during late summer and early
420 autumn. However, to fully understand push-pull dynamics, future studies should explore the
421 “pull” aspect of the hypothesis. Our results also indicate that migration distance played a role
422 in the evolution of moult-migration. Understanding such environmental drivers in species’
423 ecology is critical at this time, particularly for the chronically understudied portions of the
424 annual cycle outside of breeding (Marra et al. 2015). Given contemporary conservation
425 challenges, such as climate and land-use change, this study raises the question: how plastic
426 are species in their ability to adopt or cease a moult-migration strategy should aridity increase
427 or decrease in their breeding range (Siepielski et al. 2017)? In addition, how could changing
428 climatic conditions alter the relative strength of the “push” and/or “pull” of breeding and
429 moulting grounds, respectively? The answer to these questions could reveal which species
430 will be most resilient to ongoing environmental change.

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434

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581 **CHAPTER 3: CONTRASTING EVOLUTION OF WINTER MOULTING**
582 **STRATEGIES IN EUROPEAN AND NORTH AMERICAN PASSERINES**

583

584 **ABSTRACT**

585 Moult is critical for birds as it replaces damaged feathers and worn plumage,
586 enhancing flight performance, thermoregulation, and communication. In passerines, moult
587 generally occurs once a year, on the breeding grounds during the post-breeding period.
588 However, some species of migrant passerines that breed in the Nearctic and western
589 Palearctic regions have evolved different moulting strategies that involve moulting on the
590 overwintering grounds. Some species forego moult on the breeding grounds and instead
591 complete their prebasic moult on the overwintering grounds. Other species moult some or all
592 feathers a second time (i.e., have a prealternate moult) during the overwintering period.
593 Using phylogenetic analyses, we explored the potential drivers of the evolution of winter
594 moult in Nearctic and western Palearctic breeding passerines. Our results indicate an
595 evolutionary association between longer photoperiods on the overwintering grounds and the
596 presence of prebasic and prealternate moults on the overwintering grounds for both Nearctic
597 and western Palearctic species. We also found a relationship between having a prealternate
598 moult and wintering in open habitat for western Palearctic species. Finally, biannual moult in
599 western Palearctic passerines was linked to high primary productivity on the overwintering
600 grounds. Longer days may favour the evolution of winter prebasic moult by increasing the
601 time available for foraging and absorbing the nutrients essential for moult. Alternatively, for
602 birds undertaking a prealternate moult at the end of the overwintering period, longer days and
603 open habitats may increase exposure to feather-degrading ultra-violet radiation, necessitating
604 the replacement of feathers. Our study underlines the importance of the overwintering
605 grounds in the critical process of moult for many passerines that breed in the Nearctic and
606 western Palearctic regions.

607

608 **INTRODUCTION**

609 Moult, the replacement of old feathers by new ones, is critical for birds; fresh, high-
610 quality plumage enhances flight performance, thermoregulation, visual communication, and

611 attractiveness (Gill 2006). Hence, the timing, location, and number of moults are critical for
612 birds to grow feathers of sufficient quality and maintain relatively fresh plumage throughout
613 the annual cycle. Most migratory passerines (Order Passeriformes) that breed in the Nearctic
614 and western Palearctic regions undergo only one complete moult during the annual cycle
615 (Humphrey and Parkes 1959, Pyle et al. 1997, Jenni and Winkler 2020). This moult generally
616 occurs on the breeding grounds after nesting and is termed the prebasic moult because it
617 produces the basic plumage (Humphrey and Parkes 1959). However, when and where the
618 prebasic moult occurs can be quite variable. For example, some species or populations
619 employ a strategy in which there is a temporal overlap between moult and migration (moult-
620 migration; Tonra and Reudink 2018). This is especially common in western North America
621 where many species depart their arid breeding grounds to moult in the highly-productive
622 Mexican monsoon region prior to completing their southward migration (Pageau et al.
623 2020a). Other species migrate prior to moult and undergo the prebasic moult on the
624 overwintering grounds (Barta et al. 2008, de la Hera 2012, Kiat et al. 2019). Moult on the
625 breeding grounds appears to be the ancestral state of the prebasic moult for migratory species
626 and other strategies evolved later (Svensson and Hedenström 1999), likely in response to
627 environmental and life-history trade-offs (Pageau et al. 2020a).

628 In addition to prebasic moult, some species undergo a second moult, termed
629 prealternate, which results in the alternate or breeding plumage (Humphrey and Parkes
630 1959), at some point during the annual cycle. This usually happens in late winter/early spring
631 prior to breeding, although prealternate moult-migration has also been documented (Wright
632 et al. 2018). Generally, this moult is partial and often only involves body feathers (Jenni and
633 Winkler 2020). However, some migratory passerines undergo a complete prealternate moult,
634 replacing all their feathers on the overwintering grounds prior to spring migration (e.g.,
635 *Dolichonyx oryzivorus*, Renfrew et al. 2011; *Phylloscopus trochilus*, Underhill et al. 1992).
636 The presence of two complete moults (biannual moult) during the annual cycle is rare among
637 Nearctic migrant passerines, but more common among western Palearctic passerines
638 (Renfrew et al. 2011, Jenni and Winkler 2020). The extensive variation in moult strategies
639 among migratory passerines begs the question: which life history characteristics and/or
640 environmental factors have driven the evolution of these different moult strategies?

641 Pageau et al. (2020a) studied the evolution of moult-migration in North
642 America using phylogenetic comparative analysis and the results indicated the importance of
643 the aridity of the breeding grounds and migration distance as potential drivers of the
644 evolution of moult-migration. Phylogenetic analyses are necessary for the study of
645 evolutionary processes to correct for the non-independence among species (Felsenstein 1985;
646 Harvey and Pagel 1991; Ives and Zhu 2006), but they have not been used to look at the
647 evolution of winter moult strategies in passerines, thus leaving the drivers of winter moults
648 unresolved. In a recent study of the Nearctic-Neotropical Family Parulidae, Terrill et al. (In
649 press), concluded that structural needs driven by feather damage during the annual cycle
650 drive the evolution of prealternate moults. However, the extent to which this is the case
651 across the diverse moult strategies of passerines as a whole, remains unknown.

652 Although phylogenetic analyses have not been conducted yet to explain the
653 evolution of winter moults, potential drivers of the evolution of the prebasic moult on the
654 overwintering grounds have been hypothesized. Barta et al. (2008) created models that linked
655 winter moult in migratory birds with food seasonality; lack of resources at the end of the
656 summer combined with an abundance of resources on the overwintering grounds during
657 winter could have led to the evolution of winter moult (see also Remisiewicz et al. 2019
658 study on *Sylvia communis*). This would particularly be true for western Palearctic species
659 migrating to sub-Saharan overwintering grounds that are productive during the northern
660 fall/beginning of winter because it is the rainy season (Kiat et al. 2019, Jenni and Winkler
661 2020). An association between southern wintering latitude in Africa and winter prebasic
662 moult is also supported by Figuerola and Jovani (2001). Moulting on the overwintering
663 grounds after migration would also occur most often in long-distance migrants; longer
664 migration distance would impose a time constraint between breeding and migration and, thus,
665 could favour moult somewhere other than the breeding grounds (Kjellén, 1994, Leu and
666 Thompson 2002). De la Hera et al. (2012) recorded moult duration of 98 Nearctic passerines
667 and found that migrant species moulting on the overwintering grounds have a moult duration
668 that is as long as that of resident species moulting on breeding grounds. However, migrant
669 species moulting on the breeding grounds have a shorter moult duration. Previous studies
670 have indicated that a longer moult duration results in feathers of higher quality (e.g., Dawson
671 et al. 2000 on *Sturnus vulgaris*, Serra 2001 on *Pluvialis squatarola*, Griggio et al. 2009 on

672 *Cyanistes caeruleus*, but see de la Hera et al. 2012). Thus, it could be more advantageous for
673 long-distance migrants to moult on the overwintering grounds where there are fewer time
674 constraints, so they could grow high quality feathers.

675 The presence of a second moult during the annual cycle may be favoured due
676 to rapid degradation of the feathers due to UV exposure (Bergman 1982, Jenni and Winkler
677 2020; see studies by Svensson and Hedenström 1999 on *Phylloscopus trochilus*, Jiguet et al.
678 2019 on *Emberiza hortulana*). Thus, species living in open habitats, which would be more
679 affected by UV degradation, would be more likely to undergo a prealternate moult. This
680 would particularly be true for western Palearctic migrants, which winter in more sun-exposed
681 environments such as savannahs (Jones 1995, Rohwer et al. 2005). A complete biannual
682 moult is more common in western Palearctic migrant passerines than Nearctic migrant
683 passerines; among the latter only *Dolichonyx oryzivorus* (Renfrew et al. 2011) and
684 *Cistothorus palustris* (The Birds of the World 2020) undergo two complete moults. Rohwer
685 et al. (2005) proposed that two complete moults are rare among Nearctic migrant passerines
686 because most species winter in habitats with shade and softer foliage, resulting in relatively
687 less damage feathers than species overwintering in open habitats.

688 Here, we explore potential drivers behind the evolution of winter moults, specifically
689 comparing Nearctic and western Palearctic passerines with respect to the evolution of
690 prebasic and prealternate winter moults. We examined whether migration distance, aridity of
691 the breeding and overwintering grounds, overwintering latitude, average photoperiod and
692 habitat of the overwintering grounds were associated with the evolution of winter moults.
693 Based on previous studies, we predicted that a prebasic moult on the overwintering grounds
694 evolved in long-distance migrants for both Nearctic and western Palearctic birds (Kjellén,
695 1994, Leu and Thompson 2002). We also predicted that productive overwintering grounds
696 with a lower southern latitude would be additional drivers of this phenomenon among
697 western Palearctic species (Barta et al. 2008, Remisiewicz et al. 2019). For the prealternate
698 moult, we predicted that overwintering in open habitats and in locations where the average
699 photoperiod is longer are important for the evolution of a second moult for both Nearctic and
700 western Palearctic migrant passerines because these species would be more exposed to UV

701 radiation resulting in feather degradation (Bergman 1982, Svensson and Hedenström 1999,
702 Jiguet et al. 2019, Jenni and Winkler 2020, Terrill et al. in press).

703

704 **METHODS**

705 *Species Selection*

706 We collected data for 183 species (including 6 subspecies that vary in moulting
707 strategy) of Nearctic migratory passerines and for 115 species (including 2 subspecies) of
708 western Palearctic migratory passerines. We considered species as Nearctic migrants when
709 their breeding distribution was located in Canada or USA and when they were classified as
710 full migrants by IUCN (2020). Western Palearctic migrants are species that breed in Europe,
711 northern Africa, or western Asia.

712 *Classification of Moulting Strategies*

713 We followed the Humphrey and Parkes (1959) system to classify two types of moult:
714 prebasic moult, which results in the basic plumage and generally occurs after breeding, and
715 prealternate moult, which results in the alternate plumage and generally occurs before spring
716 migration. For the prebasic moult, we considered whether the species moulted on their
717 overwintering grounds or not as a binary variable (overwintering grounds = 1, not = 0; table
718 1). For prealternate moult, we recorded whether the moult was complete, partial or absent.
719 Thus, we created two binary response variables for prealternate moult: (A) absence or
720 presence of a prealternate moult (complete or partial) and (B) complete prealternate moult or
721 absence of a complete prealternate moult (Table 3.1). To determine the moulting strategies
722 characteristic of each species, we used various peer-reviewed journal articles (Voelker and
723 Rohwer 1998, Butler et al. 2002, Rohwer et al. 2005, Butler et al. 2006, Pyle et al. 2009, Jahn
724 et al. 2013), The Birds of the World (2020) and the Identification Guide to North American
725 Birds (Pyle 1997) for Nearctic passerines, and The Handbook of western Palearctic Birds
726 (Shirihai and Svensson 2018) for western Palearctic passerines.

727

728

729 **Table 3.1.** Number of species for Nearctic (total of 183 species) and western Palearctic (total
 730 of 115 species) passerines performing different moulting strategies: winter prebasic,
 731 prealternate, and complete prealternate moult.

	Nearctic	Palearctic
Winter prebasic	13/183 (7.1%)	8/115 (6.9%)
Prealternate	87/183 (47.5%)	56/115 (48.3%)
Complete prealternate	2/183 (1.1%)	11/115 (9.5%)

732 *Data Collection of Predictor Variables*

733 To classify the amount of primary productivity on the breeding and overwintering
 734 grounds, we calculated the normalized difference vegetation index (NDVI) using distribution
 735 maps of the breeding and overwintering grounds from BirdLife International (2018). NDVI
 736 is a measure of live green vegetation and was used to indicate the aridity of the breeding
 737 grounds during the post-breeding period (July 1 to August 31) and the overwintering grounds
 738 during the non-breeding period (September 15 to April 15). Data were available from the
 739 Application for Extracting and Exploring Analysis Ready Samples (AppEEARS Team
 740 2019). We extracted the NDVI values from 2000 to 2019 using the “Area Sample” function,
 741 chose the product MOD13A3.006 (Didan 2015), selected “Native projection”, and calculated
 742 the mean value over this time period for each species. One hundred ninety-eight distribution
 743 maps were not available from BirdLife International (2018) or unusable in AppEEARS.
 744 Instead, we created distribution maps as polygons using template maps from IUCN (2020).
 745 Methods for NDVI data collection followed those employed by Pageau et al. (2020a).

746 Migration distance was approximated as the distance (megametre; Mm) from the
 747 centroid of the breeding distribution to the centroid of the wintering distribution using the
 748 package Geosphere (Hijmans 2019) in R (R Core Team 2019). Centroid values were
 749 calculated in decimal degrees using polygon maps provided by BirdLife International (2018)
 750 in ArcMap. One hundred seventy maps were unavailable from BirdLife International and the
 751 centroid values were calculated by creating polygons in Google Earth pro using template
 752 maps from IUCN (2020) and processing the polygons in Earth Point (2020).

753 Average photoperiods at the overwintering grounds were determined using each
 754 species’ latitude and longitude of the centroid of their overwintering distribution with the
 755 National Research Council of Canada (2020) sunset/sunrise calculator. Photoperiods on the

756 overwintering grounds were retrieved from September 15th to April 15th 2018/2019 and
757 averaged for each species. Latitude of the overwintering grounds (decimal degrees) was also
758 determined using the centroids.

759 We categorized the type of habitat for the overwintering grounds using BirdLife Data
760 Zone (BirdLife International 2020). We prioritized the habitats considered “major” by
761 BirdLife International, then “suitable” and we categorized the habitat in four major
762 categories: dense (forest, shrubland), open (grassland, savanna, open woodland, rocky areas),
763 water (wetland, marine), and generalist. We classified species as generalist when two or more
764 major habitats were used. Habitat classification followed methods employed by Pageau et al.
765 (2020b).

766 *Phylogeny*

767 Using BirdTree.org (Jetz et al. 2012), we downloaded 1000 possible trees from
768 “Ericson All Species: a set of 10000 trees with 9993 OTUs each” (Ericson et al. 2006) for a
769 phylogeny subset of 177 Nearctic species and a subset of 113 western Palearctic species.
770 Using TreeAnnotator V.1.10.4 (Rambaut and Drummond 2018), we then created the
771 maximum clade credibility trees for the Nearctic and Palearctic species with our 1000 trees
772 using 1% burn-in (as states) and mean heights for node heights. We added the subspecies (6
773 Nearctic, 2 Palearctic) in R (R Core Team 2019) using the package phytools (Revell 2012) to
774 obtain a maximum clade credibility tree of 183 species and subspecies for the Nearctic and
775 115 for the western Palearctic. We used trees including the species and subspecies for all our
776 analyses. The visual representations of the phylogenies (Figures 3.1 and 3.2) were created
777 using the phytools package (Revell 2012).

778 *Statistical Analysis*

779 For each response variable (prebasic winter, prealternate, and complete prealternate
780 moult), we analysed the western Palearctic and Nearctic passerines separately. Note that we
781 could not analyse the presence of a complete prealternate moult in Nearctic passerines
782 because only two species in North America exhibit a complete prealternate moult. Prior to
783 our analyses, we tested for collinearity; migration distance, average photoperiod, and
784 wintering latitude were highly correlated ($r > 0.5$), but were never expected to be
785 simultaneously present in the same model. Next, we used phylogenetic logistic linear models

786 to test the predictors and created all the possible models (total of 31 models per response
787 variable). We selected the best models using Akaike information criterion (AIC) and
788 determined that models were similar if they differed by $<4 \Delta AIC$. The Akaike weights were
789 obtained using the qpcR package (Spiess 2018) and the R2 using the function R2.lik from the
790 rr2 package (Ives and Daijiang 2018). Finally, we examined the 95% confidence intervals of
791 the parameter estimates of every predictor included in the top models to assess which
792 variables were informative. Analyses were conducted in R (R Core Team 2020) using the
793 package phyloglm (Ho and Ane 2014). The “logistic_MPLE” method was applied with a btol
794 of 35, a log.alpha.bound of 10, and 100 bootstraps.

795

796 **RESULTS**

797 *Prebasic winter moult*

798 For the western Palearctic species, the top models predicting the presence of a
799 prebasic winter moult included NDVI of the breeding and non-breeding grounds and average
800 photoperiod on the overwintering grounds (Table 3.2). For the Nearctic species, the same
801 three variables were also present in the top models, but with the addition of migration
802 distance (Table 3.2). For both western Palearctic and Nearctic passerines, only photoperiod
803 had a 95% confidence interval that did not overlap zero (Table 3.3). The parameter estimates
804 were both positive (western Palearctic: 2.11, Nearctic: 1.48) which indicates that longer
805 photoperiods were evolutionarily associated with a prebasic moult on the overwintering
806 grounds in both of these groups (Figures 3.1 and 3.2). Latitude was marginally significant for
807 western Palearctic species and indicated that more southern overwintering grounds were
808 associated with winter prebasic moult.

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814 **Table 3.2.** Top ranked models (<4 AIC units from top model) explaining a prebasic moult on
 815 the overwintering grounds and the presence of a second moult (prealternate), which can be
 816 completed, in western Palearctic and Nearctic passerines. NDVI breed = NDVI breeding
 817 grounds, NDVI w = NDVI overwintering grounds, migration distance = migration distance
 818 between the centroid of the breeding and overwintering grounds, day length = average day
 819 length at the centroid of the wintering ground between September 15 and April 15, latitude =
 820 latitude of the centroid of the overwintering grounds, habitat w = main habitat used on the
 821 overwintering grounds.

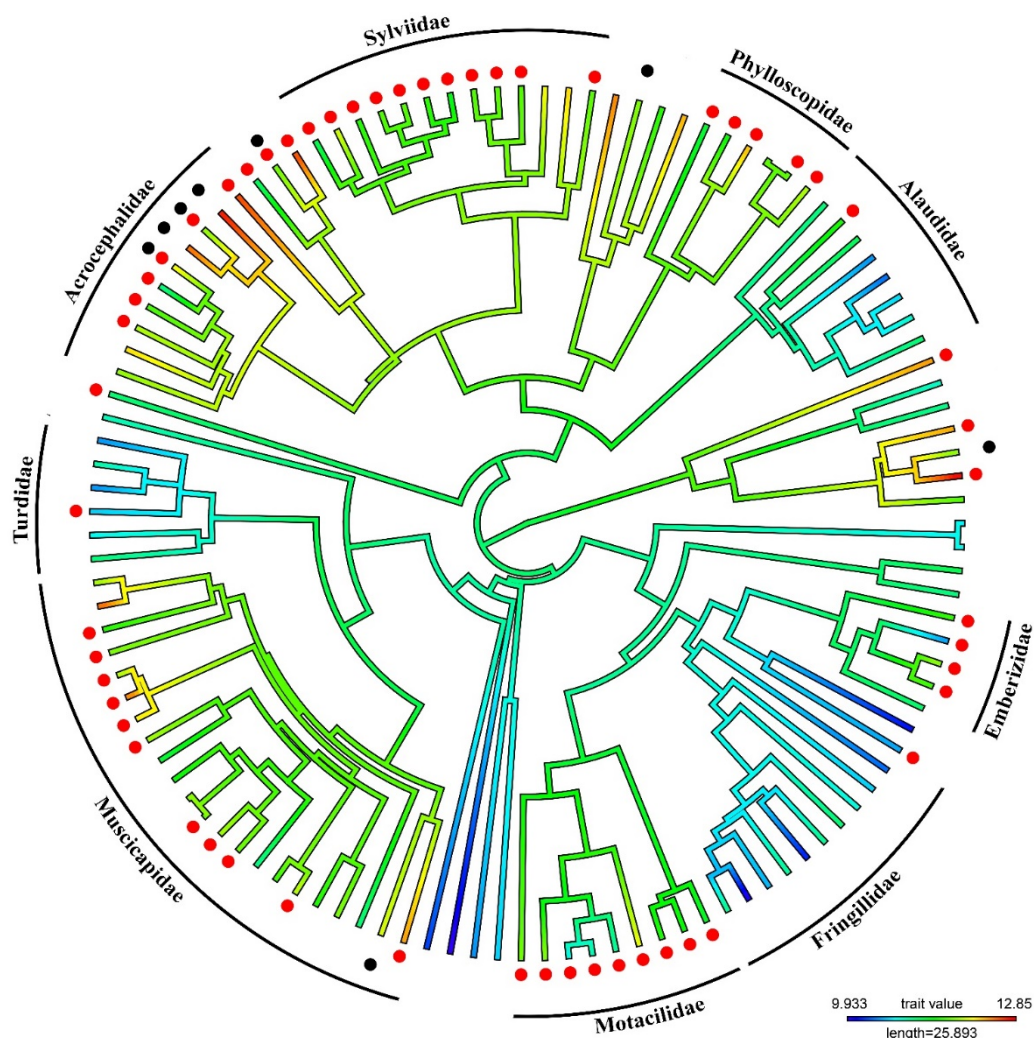
Moult	Region	Top models	AIC	ΔAIC	w	R²	
Prebasic winter	Western	NDVI breed + latitude	50.14	0	0.40	0.33	
		Paleartic	NDVI breed + day length	50.59	0.45	0.32	0.32
			NDVI breed + NDVI w + latitude	51.93	1.79	0.16	0.33
			NDVI breed + NDVI w + day length	52.42	2.28	0.13	0.32
		Nearctic	Day length	84.12	0	0.19	0.26
			Latitude	84.37	0.25	0.17	0.25
			NDVI breed	85.24	1.12	0.11	0.24
			NDVI w	85.25	1.13	0.11	0.24
			Migration distance	85.35	1.23	0.10	0.24
			NDVI w + day length	86.11	1.99	0.07	0.26
			NDVI breed + latitude	86.38	2.26	0.06	0.25
			NDVI w + latitude	86.47	2.35	0.06	0.25
			NDVI w + migration distance	87.43	3.31	0.04	0.24
			NDVI breed + migration distance	87.54	3.42	0.03	0.24
	NDVI breed + NDVI w	87.55	3.43	0.03	0.24		
	NDVI breed + NDVI w + day length	88.04	3.92	0.03	0.26		
Prealternate	Western	Day length + habitat w	135.32	0	0.31	0.36	
		Paleartic	Average day length	136.78	1.76	0.15	0.29
			NDVI w + day length + habitat w	137.43	2.11	0.11	0.36
			NDVI breed + day length + habitat w	137.47	2.15	0.11	0.36
			NDVI w + day length	137.98	2.66	0.08	0.30
			NDVI breed + day length	138.73	3.41	0.06	0.29
			Latitude + habitat w	138.97	3.65	0.05	0.33
			NDVI w + latitude + habitat w	139.05	3.73	0.05	0.34
			NDVI breed + NDVI w + day length + habitat w	139.17	3.85	0.04	0.36
			NDVI breed + latitude + habitat w	139.31	3.99	0.04	0.34
		Nearctic	Day length	221.8	0	0.13	0.25
			Migration distance	221.8	0	0.13	0.25
			NDVI w	222	0.2	0.12	0.24
			NDVI breed + migration distance	222.1	0.3	0.12	0.26
	Latitude		222.3	0.5	0.10	0.24	

		NDVI breed + NDVI w + migration distance	223.2	1.4	0.07	0.26
		NDVI breed + latitude	223.4	1.6	0.06	0.25
		NDVI breed	223.5	1.7	0.06	0.24
		NDVI w + migration distance	224	2.2	0.04	0.24
		NDVI w + latitude	224	2.2	0.04	0.24
		NDVI w + day length	224.4	2.6	0.04	0.24
		Migration distance + habitat w	224.9	3.1	0.03	0.26
		NDVI breed + NDVI w	225.2	3.4	0.02	0.24
		Habitat w	225.4	3.6	0.02	0.25
Complete	Western	NDVI w + latitude	56.61	0	0.63	0.38
prealternate	Palaearctic	NDVI breed + latitude	57.68	1.07	0.37	0.40

823 **Table 3.3.** Model-averaged parameter estimates and 95 % confidence intervals for variables included in the top-ranked models (<4
 824 AICc units of best model) explaining a prebasic moult on the overwintering grounds and the presence of a second moult
 825 (prealternate), which can be completed, in western Palearctic and Nearctic passerines. Values in bold indicate that the 95 % CI did
 826 not overlap zero. See table 2 for variable's definition.

	Prebasic winter		Prealternate		Prealternate completed
	Western Palearctic	Nearctic	Western Palearctic	Nearctic	Western Palearctic
NDVI breed	-3.07 (-8.77, 0.0009)	0.001 (-2.21, 2.88)	-1.11 (-2.98, 0.047)	-0.32 (-1.66, 1.18)	2.71 (-4.19, 6.18)
NDVI w	2.53 (-3.85, 6.82)	0.44 (-2.86, 3.35)	0.73 (-1.94, 2.53)	1.83 (-0.14, 4.26)	5.52 (1.08, 7.75)
Migration distance		0.021 (-0.30, 0.26)		0.14 (-0.070, 0.33)	
Day length	2.11, (2.02, 2.20)	1.48 (1.44, 1.64)	1.28 (1.17, 1.36)	0.50, (0.44, 0.59)	
Latitude	-0.32 (-0.75, 0)	-0.24 (-0.57, 0.14)	-0.035 (-0.042, 0)	-0.14 (-0.37, 0.051)	-0.09 (-0.09, 0)
Habitat - Generalist			1.33 (0.36, 2.46)	0.0066 (-0.55, 0.64)	
Habitat - Water			0.50 (-0.90, 1.74)	-0.15 (-1.08, 0.61)	
Habitat - Open			1.88 (0.17, 3.75)	0.75 (-0.30, 1.88)	

828



829

830 **Figure 3.1.** Phylogeny of the 115 species and subspecies of western Palearctic passerines.

831 The color of the branches represents the average day length where red is longer day length.

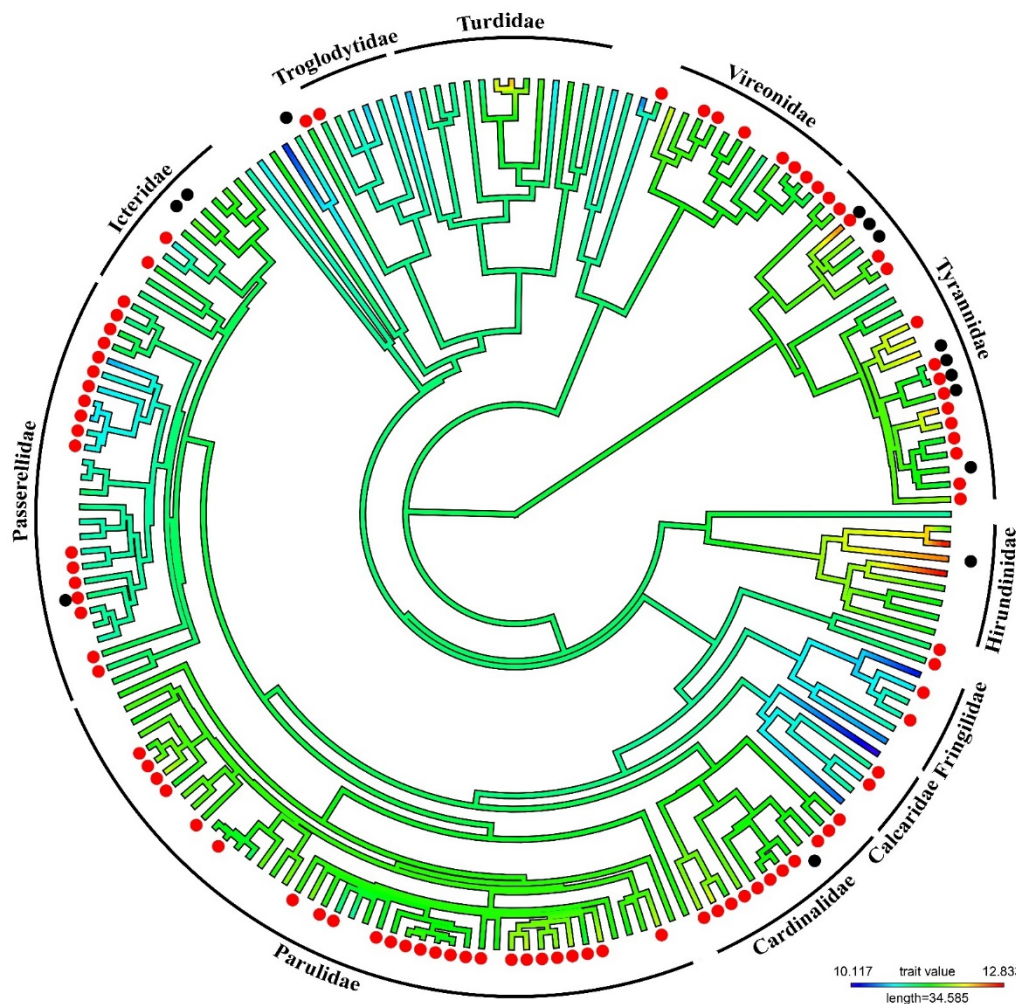
832 The red dots indicate species that have a prealternate moult while the black dots indicate a

833 prebasic moult on the overwintering grounds. We labelled passerine families with more than

834 5 members.

835

836



837

838 **Figure 3.2.** Phylogeny of the 183 species and subspecies of Nearctic passerines. The color of
 839 the branches represents the average day length where red is longer day length. The red dots
 840 indicate the species with a prealternate moult while the black dots indicate a prebasic moult
 841 on the overwintering grounds. We labelled passerine families with more than 5 members.

842

843 *Presence of a prealternate moult*

844 The top models explaining the presence of a prealternate moult in western Palearctic
 845 passerines included the following variables: NDVI of the breeding grounds and
 846 overwintering grounds, photoperiod, latitude, and habitat of the overwintering grounds
 847 (Table 3.2). Of these five variables, the confidence intervals of average photoperiod,
 848 generalist habitat, and open habitat did not overlap zero (Table 3.3). The parameter estimates
 849 of average photoperiod (1.28), generalist habitat (1.33), and open habitat (1.88) all indicated

850 a positive association with prealternate moult; longer photoperiod, species wintering in open
851 habitat types or being generalist in their selection of habitat were evolutionarily associated
852 with the presence of a prealternate moult (Figure 3.1). For the Nearctic passerines, the top
853 models contained all the variables (NDVI breeding and overwintering grounds, migration
854 distance, photoperiod, latitude, and habitat of the overwintering grounds), but only the
855 confidence intervals of photoperiod did not overlap zero (Table 3.2, 3.3). Longer photoperiod
856 (0.50) was evolutionarily associated with the presence of a prealternate moult in Nearctic
857 passerines (Figure 3.2). Latitude was marginal for western Palearctic passerines with
858 southern latitude associated with prealternate moult.

859 *Presence of a complete prealternate moult*

860 Western Palearctic passerines that underwent a complete prealternate moult had two
861 top models that both contained latitude of the overwintering grounds coupled with either
862 NDVI of the breeding grounds or NDVI of the overwintering grounds (Table 3.2). However,
863 only NDVI of the overwintering grounds had a 95% confidence interval that did not overlap
864 zero (Table 3.3). The parameter estimate of this variable (5.52) suggests that higher NDVI on
865 the overwintering grounds, which is indicative of high primary productivity, was
866 evolutionarily associated with the presence of a complete prealternate moult. Latitude was
867 marginal and indicated that more southerly latitudes may be evolutionarily associated with
868 complete prealternate moult.

869

870 **DISCUSSION**

871 The aim of this study was to explore the potential drivers of the evolution of winter
872 moults in Nearctic and western Palearctic passerines. We examined the evolution of prebasic
873 moult on the overwintering grounds, the presence of a prealternate moult (a second moult) on
874 the overwintering grounds, and the presence of a complete prealternate moult (a biannual
875 moult). We found that the evolution of a prebasic moult on the overwintering grounds is
876 evolutionarily associated with longer average photoperiods on the overwintering grounds for
877 Nearctic as well as western Palearctic passerines. Our results also indicate, for western
878 Palearctic passerines, that longer photoperiods on the overwintering grounds and species
879 living in open habitats or being generalists in their habitat choice exhibit an evolutionary

880 association with the presence of prealternate moult. For Nearctic passerines, only longer
881 photoperiods were a potential driver of the evolution of a prealternate moult. Finally, the
882 evolution of a complete prealternate moult (biannual moult) in western Palearctic passerines
883 is associated with a higher NDVI on the overwintering grounds, which indicates more live
884 green vegetation and, thus, higher primary productivity. Collectively, these results indicate
885 the powerful selective force of overwintering conditions in the evolution of moult strategies.

886 The evolution of the prebasic moult on the overwintering grounds for both Nearctic
887 and western Palearctic migrants is influenced by longer photoperiod in this area. This result
888 was unexpected because we predicted that longer migration distance (Kjellén, 1994, Leu and
889 Thompson 2002), and food seasonality (Barta et al. 2008, Remisiewicz et al. 2019) would be
890 the primary drivers of the evolution of winter prebasic moult. Additionally, we were not
891 expecting longer photoperiods to be a potential driver of prebasic moult because we
892 hypothesized that longer photoperiods would expose feathers to more UV radiation and, as a
893 consequence, result in faster feather degradation. However, longer photoperiods could have
894 some benefits by reducing the costs associated with moult by increasing the duration of the
895 absorptive state for nutrients essential for moult (Murphy and King 1991, Renfrew et al.
896 2011). Thus, some species might have evolved a winter prebasic moult strategy to take
897 advantage of longer photoperiods on the overwintering grounds compared to shorter
898 daylights in fall on the summer grounds.

899 The evolution of the prealternate moult in Nearctic and western Palearctic migrants
900 has been proposed to result from the amount of feather degradation caused by the habitat
901 where they overwinter (Rohwer et al. 2005, Terrill et al. In press). In overwintering grounds
902 with longer days throughout the winter, both Nearctic and western Palearctic passerines may
903 have evolved prealternate moults to cope with increased feather wear from UV light
904 exposure (Bergman 1982, Barta et al 2008). From our data, for western Palearctic migrant
905 passerines, species that inhabited open habitats, or were generalists, were more likely to
906 evolve a prealternate moult. Open habitats increase the amount of wear on feathers since
907 conditions are harsher and the habitat is more exposed to UV light (Rohwer et al. 2005).
908 Generalist species are those that inhabit multiple types of habitats, such as open and dense
909 habitat; thus, the open habitat component included in the category generalist could explain

910 why species with a generalist strategy were more likely to evolve a prealternate moult.
911 Habitat was not a significant variable for Nearctic passerines; these passerines generally
912 overwinter in tropical habitats with softer foliage, which does not damage feathers (Rohwer
913 et al. 2005). In summary, the prealternate moult, which is often incomplete, seems to have
914 evolved in species affected by strong feather wear and in need of replacing specific feathers
915 to maximise fitness. This result supports Terrill et al. (In press) findings, which identified
916 feather wear as a driver of the evolution of prealternate moult in Parulidae.

917 The presence of a complete prealternate moult in western Palearctic passerines
918 appears to have evolved in species overwintering in productive areas with more live green
919 vegetation. This runs counter to our hypothesis; we predicted that a complete prealternate
920 moult would have evolved in species wintering in harsher and sun-exposed environments that
921 damage the feathers faster, hence the need to replace them in a second moult (Jones 1995,
922 Rohwer et al. 2005, Jenni and Winkler 2020). More live green vegetation could have driven
923 the evolution of a complete prealternate moult due to the abundance of resources and
924 nutrients it would provide (Barta et al. 2008). Moulting is an energetically-expensive activity
925 (Murphy and King 1991, Dietz et al. 1992, Lindström et al. 1993, Jenni and Winkler 2020);
926 thus, birds might be able to afford a second moult during the annual cycle if the resources are
927 available and abundant and the cost of replacing new feathers is low, resulting in a net fitness
928 benefit. Unlike more common partial prealternate moults, complete prealternate moult
929 includes replacement of all flight feathers. Thus, being able to moult plumage twice during
930 the annual cycle would potentially enhance flight performance, in addition to
931 thermoregulation, visual communication, and attractiveness (Gill 2006).

932 We could not repeat the complete prealternate moult analysis with Nearctic
933 passerines because only two species that breed in North America have two complete moults
934 during the annual cycle. This low number is perhaps surprising since we observed that a
935 higher NDVI of the overwintering grounds is evolutionarily associated with the complete
936 prealternate moult in western Palearctic passerines. Nearctic passerines generally winter in a
937 more tropical environment (Rohwer et al. 2005) where the NDVI is higher than for western
938 Palearctic species. Thus, we could expect that more Nearctic passerines would undergo a
939 complete prealternate moult. Even if the resources are available for a second moult on the

940 overwintering grounds, Nearctic passerines might not undertake a prealternate moult if it is
941 not necessary to spend the extra time and energy require to moult. Then, what other factors
942 than higher NDVI of the overwintering grounds drive western Palearctic passerines to
943 undergo a complete prealternate moult? The drivers behind the evolution of a second
944 complete moult in Nearctic passerines could be completely different than those for western
945 Palearctic passerines because the only two Nearctic species that have two complete moult
946 live in grasslands (*Dolichonyx oryzivorus*) and emerging wetlands (*Phylloscopus trochilus*)
947 which would have low NDVI (Birds of the World 2020).

948 Molt is a complex process that affects birds over multiple seasons and impacts many
949 aspects of their life such as flight, thermoregulation, communication and mate selection (Gill
950 2006). Therefore, the evolution of moulting strategies was likely influenced by multiple
951 variables impacting at least one function of the plumage. In this study, we focused on the
952 importance of having a fresh plumage of high quality, but we did not examine the role of
953 sexual selection in driving the evolution of moult strategies, particularly prealternate moult.
954 For future work, it would be important to examine feather colouration and degree of sexual
955 dichromatism, especially as it may play an important role in the evolution of prealternate
956 moult which generally happens before spring migration and breeding. Terrill et al. (In press)
957 found that, in Parulidae, seasonal dichromatism can only evolve when a prealternate moult
958 already exists; it would thus be interesting to examine the relation between dichromatism and
959 prealternate moult across all passerines.

960 In conclusion, our results indicate the importance of the overwintering grounds to the
961 evolution of moulting strategies in Nearctic and western Palearctic migratory passerines.
962 What remains to be seen is how the availability of resources, and their influence on the costs
963 of feather production and plumage quality, have played a role in these systems. It is very
964 important to understand the drivers behind the evolution of different moulting strategies
965 because the quality of the moult impacts fitness throughout the annual cycle (Nilsson and
966 Svensson 1996, Dawson et al. 2000, Harrison et al. 2011). There is a need for a full annual
967 cycle focus in animal ecology to effectively conserve populations (Marra et al. 2015). In that
968 context, our findings indicate that rapid changes in conditions on the overwintering grounds
969 (e.g., through climate change and/or habitat loss) could have substantial impacts on the

970 selective forces shaping moult strategies, potentially requiring populations to have sufficient
971 plasticity or adaptive capacity to overcome impacts on survival and reproduction.
972 Alternatively, the strong role of static components of the abiotic environment, such as
973 photoperiod, in the evolution of moult strategies may preclude some species from responding
974 to changing biotic conditions, with unknown consequences for fitness.

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1167 **CHAPTER 4: EVOLUTION OF ALTITUDINAL MIGRATION IN PASSERINES IS**
1168 **LINKED TO DIET**

1169 Published in Ecology and Evolution

1170 **ABSTRACT**

1171 Bird migration is typically associated with a latitudinal movement from north to south
1172 and vice versa. However, many bird species migrate seasonally with an upslope or
1173 downslope movement in a process termed altitudinal migration. Globally, 830 of the 6579
1174 Passeriformes species are considered altitudinal migrants and this pattern has emerged
1175 multiple times across 77 families of this order. Recent work has indicated an association
1176 between altitudinal migration and diet, but none have looked at diet as a potential
1177 evolutionary driver. Here, we investigated potential evolutionary drivers of altitudinal
1178 migration in passerines around the world by using phylogenetic comparative methods. We
1179 tested for evolutionary associations between altitudinal migration and foraging guild and
1180 primary habitat preference in passerines species worldwide. Our results indicate that foraging
1181 guild is evolutionarily associated with altitudinal migration, but this relationship varies across
1182 zoogeographical regions. In the Nearctic, herbivorous and omnivorous species are associated
1183 with altitudinal migration, while only omnivorous species are associated with altitudinal
1184 migration in the Palearctic. Habitat was not strongly linked to the evolution of altitudinal
1185 migration. While our results point to diet as a potentially important driver of altitudinal
1186 migration, the evolution of this behaviour is complex and certainly driven by multiple
1187 factors. Altitudinal migration varies in its use (for breeding or moulting), within a species,
1188 population, and even at the individual level. As such, the evolution of altitudinal migration is
1189 likely driven by an ensemble of factors, but this study provides a beginning framework for
1190 understanding the evolution of this complex behaviour.

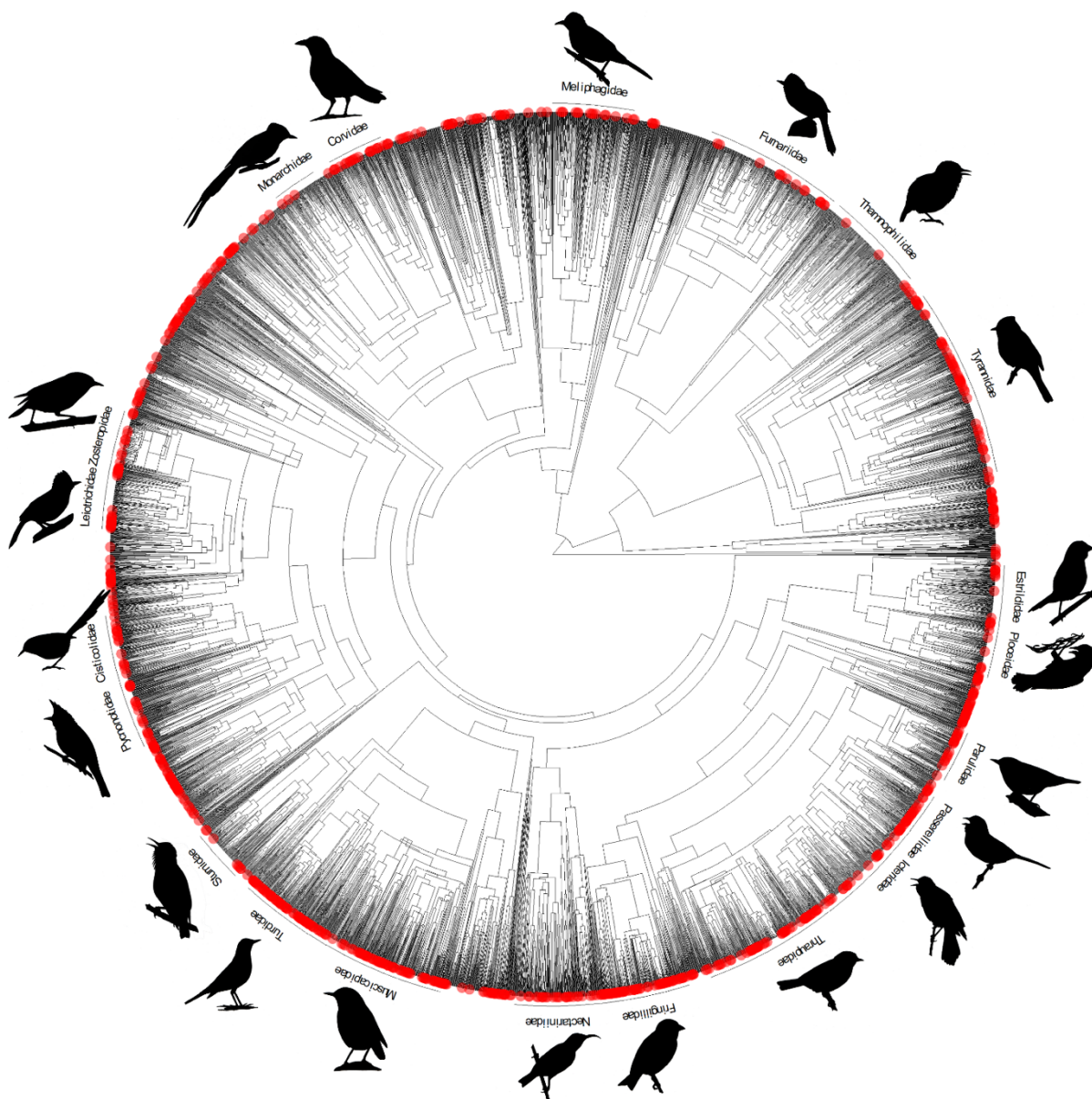
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1192 **INTRODUCTION**

1193 Altitudinal migration is generally described as a seasonal movement from lower
1194 elevations to higher elevations for the breeding season and a downslope movement for the
1195 non-breeding season (Barçante, Vale, & Alves, 2017; Hayes, 1995; Mackas et al., 2010).
1196 Some species also engage in altitudinal movements to reach moulting grounds (Rohwer,

1197 Rohwer, & Barry, 2008; Wiegardt, Wolfe, Ralph, Stephens, & Alexander, 2017). Altitudinal
1198 migration has been observed in a broad diversity of bird species; in total, 1238 species across
1199 130 families of birds have been described as altitudinal migrants (Barçante et al., 2017),
1200 suggesting repeated independent evolution of this behaviour (Figure 4.1). There are three
1201 main advantages ascribed to altitudinal migration: reduction in the risk of predation (Boyle,
1202 2008a), avoidance of harsh climatic conditions (Boyle, 2008b; Boyle, Norris, & Guglielmo,
1203 2010; Hahn, Sockman, Nreuner, & Morton, 2004), and tracking of food resources (Chaves-
1204 Campo, 2004; Kimura, Yumoto, & Kikuzawa, 2001; Levey, 1988; Loiselle, & Blake, 1991;
1205 Solorzano, Castillo, Valverde, & Avila, 2000).

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1208 **Figure 4.1.** Phylogeny of all Passeriformes and occurrences of altitudinal migration
 1209 represented by red circles. Speciose families (>100 species) names and silhouettes are shown
 1210 along the outside of the phylogeny.

1211 Most studies on altitudinal migration have focused on the food abundance hypothesis
 1212 rather than predation and climatic conditions, which are extremely challenging to study
 1213 across a wide range of species and habitats. Some studies on altitudinal migration have
 1214 provided evidence that frugivorous bird abundance is linked to fruit and flower abundance
 1215 (Chaves-Campo, 2004; Kimura et al., 2001; Levey, 1988; Loiselle, & Blake, 1991) while
 1216 others have shown no evidence of this phenomenon (Boyle, 2010; Hart et al., 2011; Papeş,

1217 Peterson, & Powell, 2012; Rosselli, 1994). Boyle (2017), Chaves-Campos (2004), Kimura et
1218 al. (2001) and Pratt, Smith and Beck (2017) suggested that food abundance drives uphill
1219 migration only, but this might depend on the species since Loiselle and Blake (1991)
1220 described downhill movement for some frugivorous species in Costa Rica when food was
1221 decreasing.

1222 If altitudinal migration evolved as a strategy to track food resources, we would
1223 predict a link between diet (foraging guild) and altitudinal migration; however, the evidence
1224 for this relationship remains unclear. Frugivory has been suggested as a driver of altitudinal
1225 migration, in part because frugivorous altitudinal migrants have been observed more
1226 frequently at higher elevations in Costa Rica (Blake, & Loiselle, 2000; Boyle, Conway, &
1227 Bronstein, 2011) and Nepal (Katuwal et al., 2016). However, Barçante et al. (2017)
1228 examined the foraging guild of all altitudinal migrant birds and showed that invertivorous
1229 altitudinal migrants are most abundant worldwide, except in the Neotropics where frugivores
1230 and nectivores are more abundant. Despite the fact that insect abundance in temperate
1231 regions is often posited as a major driver of the evolution of long distance migration, little
1232 research has been dedicated to the role of insect abundance in the study of altitudinal
1233 migration even though insect intake might be crucial during the breeding season (Chaves-
1234 Campos, 2004; Levey, 1988) and invertivore bird species have been shown to vary in
1235 elevation seasonally in mountainous environments, such as Nepal (Katuwal et al., 2016).

1236 Altitudinal migration has been observed in every zoogeographical region in the world
1237 (Barçante et al., 2017) although some hotspots seem to host a higher proportion of altitudinal
1238 migrants, such as the Himalayas and western North America (Boyle, 2017). It is important to
1239 note, however, that some of this variation in the proportion of altitudinal migrants could
1240 result from a difference in sampling efforts across the world (Barçante et al., 2017).
1241 Alternatively, environmental conditions in those regions, such as habitat availability and
1242 seasonality, may also favor the evolution of altitudinal migration.

1243 Our goal was to examine potential drivers of the evolution of altitudinal migration in
1244 passerines. The order Passeriformes represents approximately half of the avifauna and 13%
1245 of them are described as altitudinal migrants, making them a good choice for this study. Of
1246 the 6579 passerines species and subspecies recorded in this study, 830 are considered

1247 altitudinal migrants; these are distributed across 77 of the 137 families of Passeriformes
1248 (Figure 4.1). Using a speciose and globally distributed group of birds, we conducted large-
1249 scale phylogenetic comparative analyses to examine evolutionary associations between
1250 altitudinal migration and diet (foraging guild) and habitat. In addition, we asked whether
1251 these associations differ depending on the zoogeographic region. We expected that
1252 frugivorous and nectivorous species were driven toward altitudinal migration in the
1253 Neotropics because they were tracking fruit and flower abundance, which varies seasonally
1254 (Barçante et al., 2017; Chaves-Campo, 2004; Kimura et al., 2001; Levey, 1988; Loiselle, &
1255 Blake, 1991). For every other region, invertivorous species would be driven toward
1256 altitudinal migration (Barçante et al., 2017). We also expected altitudinal migration to be
1257 evolutionary associated with forest habitats in the Neotropics because altitudinal migrants in
1258 Costa Rica (Stiles & Clark, 1989; Stiles, 1988) and southeastern Brazil (Stotz, unpubl. – see
1259 Stotz et al., 1996), for instance, include a high number of restricted-range and forest-
1260 dependent species.

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1262 **METHODS**

1263 *Data Collection*

1264 We compiled data for species and subspecies of songbirds across the world, from
1265 supplementary material in Wilman et al. (2014) and Barçante et al. (2017), and data mining
1266 from two online databases: IUCN Redlist and Birdlife Data Zone (retrieved in November
1267 2018). All entries were checked for nomenclature inconsistencies. Our universe consists of
1268 all 6579 passerines in the IUCN Redlist database, downloadable from their website
1269 <https://www.iucnredlist.org/search> after restricting (advanced) searches by taxonomy
1270 selecting, in the "search filters" option [Kingdom=Animalia; Phylum=Chordata; Class=Aves;
1271 Order=Passeriformes]. We associated four variables to each species: altitudinal migration
1272 status, primary habitat preference, foraging guild and zoogeographic region.

1273 A species was classified in our dataset as an altitudinal migrant if its (common or
1274 scientific) name is listed in Barçante et al. (2017) either as altitudinal (238 species) or
1275 probable altitudinal migrant (592 species). Birdlife Data Zone provides, among many other
1276 items of information, the list of preferred breeding and non-breeding habitats of a given

1277 species on the webpage http://datazone.birdlife.org/species/factsheet/common_name-
1278 [scientific_name/details](http://datazone.birdlife.org/species/factsheet/common_name-scientific_name/details) (where spaces are replaced by the character "-" for its common and
1279 scientific names). Considering the great variety of habitats, we only used the major natural
1280 breeding habitat for each species and collapsed habitats into four major categories: dense
1281 habitat (forest + shrubland, 4635 species), open habitat (grassland + savanna + open
1282 woodland + rocky areas, 563 species), water habitat (wetland + marine, 164 species) and
1283 generalist (1217 species). Species that occupied two or more major categories were classified
1284 as generalists.

1285 Foraging guild data were obtained from Wilman et al. (2014) where species are
1286 distributed among five categories. Our dataset contained 754 frugivore/nectarivore species,
1287 547 species eating seed/plant material, 4018 invertivore species, 1213 omnivore species, and
1288 20 species eating vertebrate/fish/scavenger. 71 species had no information on Wilman et al.
1289 (2014) and were classified with information from the Handbook of the Birds of the World
1290 Alive (del Hoyo, Elliott, Sargatal, Christie, & Kirwan, 2019) (this was the case for 47
1291 species) or using the foraging guild of the closest related species (24 species).

1292 To build the zoogeographic region of the breeding distribution, we downloaded from
1293 IUCN Redlist website 13 lists of Passeriformes, each with all Passeriformes observed on a
1294 specific "Land Region" (selected in the "search filters" option) and translated those regions to
1295 a reduced set of zoogeographical regions as follows: "Caribbean islands" = Neotropical,
1296 "Antarctica" = Neotropical, "East Asia" = Indomalayan, "Europe" = Palearctic,
1297 "Mesoamerica" = Neotropical, "North Africa" = Checked individually; "North America" =
1298 Nearctic. "North Asia" = Palearctic. "Oceania" = Australian. "South America" = Neotropical,
1299 "South and Southeast Asia" = Indomalayan, "Sub-Saharan Africa" = Afrotropical, "West and
1300 Central Asia" = Checked individually. Species residing in more than one zoogeographical
1301 region were classified as "Widespread" after manual investigation of their breeding
1302 distribution maps in the IUCN website. Our dataset consists of 1298 Afrotropical (11%
1303 migrant), 816 Australasian (6% migrant), 1422 Indomalayan (17% migrants), 288 Nearctic
1304 (31% migrant), 2387 Neotropical (10% migrant), 342 Palearctic (20% migrant) and 26
1305 Widespread (42% migrant) species.

1306

1307 *Phylogeny*

1308 We downloaded the first 1000 trees from Hackett backbone phylogenetic trees
1309 (Hackett et al., 2008). Hackett backbone phylogenetic trees are available from BirdTree.org
1310 (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012). The trees were read in Rstudio (RStudio
1311 Team, 2016) using the ape package (Paradis, & Schliep, 2018). We trimmed 4105 species to
1312 only keep Passeriformes species using the drop.tip function in the phytools package (Revell,
1313 2012). Using TreeAnnotator (Rambaut, & Drummond, 2018), a maximum clade credibility
1314 tree was created with 1% burn-in and mean heights. The final tree used in the analysis
1315 consisted of 5888 species and 691 subspecies. Most subspecies are considered full species by
1316 IUCN (2019), but are not included in Birdtree.org phylogenies (Jetz et al., 2012). Since they
1317 were absent from the Hackett backbone phylogeny, subspecies were added to the tree by
1318 matching the genus and species names of the sister species (e. g. *Acrocephalus luscinius*
1319 *hiwae* matched with *Acrocephalus luscinius*), which created polytomies inside the
1320 phylogeny.

1321 *Statistical Analysis*

1322 To examine evolutionary associations between altitudinal migration and life history
1323 characteristics, we used phylogenetic generalized least squares (pgls) analyses from the
1324 packages ape (Paradis, & Schliep, 2018) and nlme (Pinheiro, Bates, DebRoy, Sarkar, & R
1325 Core Team, 2019). Brownian correlation and the maximum likelihood method were applied
1326 to each model. The models consisted of the response variable (altitudinal migration) coupled
1327 with each predictor individually (diet, habitat, region), predictors paired together, or all
1328 predictors together. Two models also included an interaction; one between diet and region
1329 and one between habitat and region. The interaction was included to test if the patterns of
1330 guild vary from one zoogeographical region to another as shown by Barcante et al. (2017);
1331 the same was applied to habitat. For the models with the interaction, we had to merge
1332 frugivore/nectarivore with seed/plant material and vertebrate/fish/scavenger with invertivore,
1333 resulting in three diet categories: herbivore, omnivore, and invertivore. We ranked the
1334 models using Akaike's information criterion (AIC). We considered the top models
1335 competitive if they differed by less than 4 AIC units.

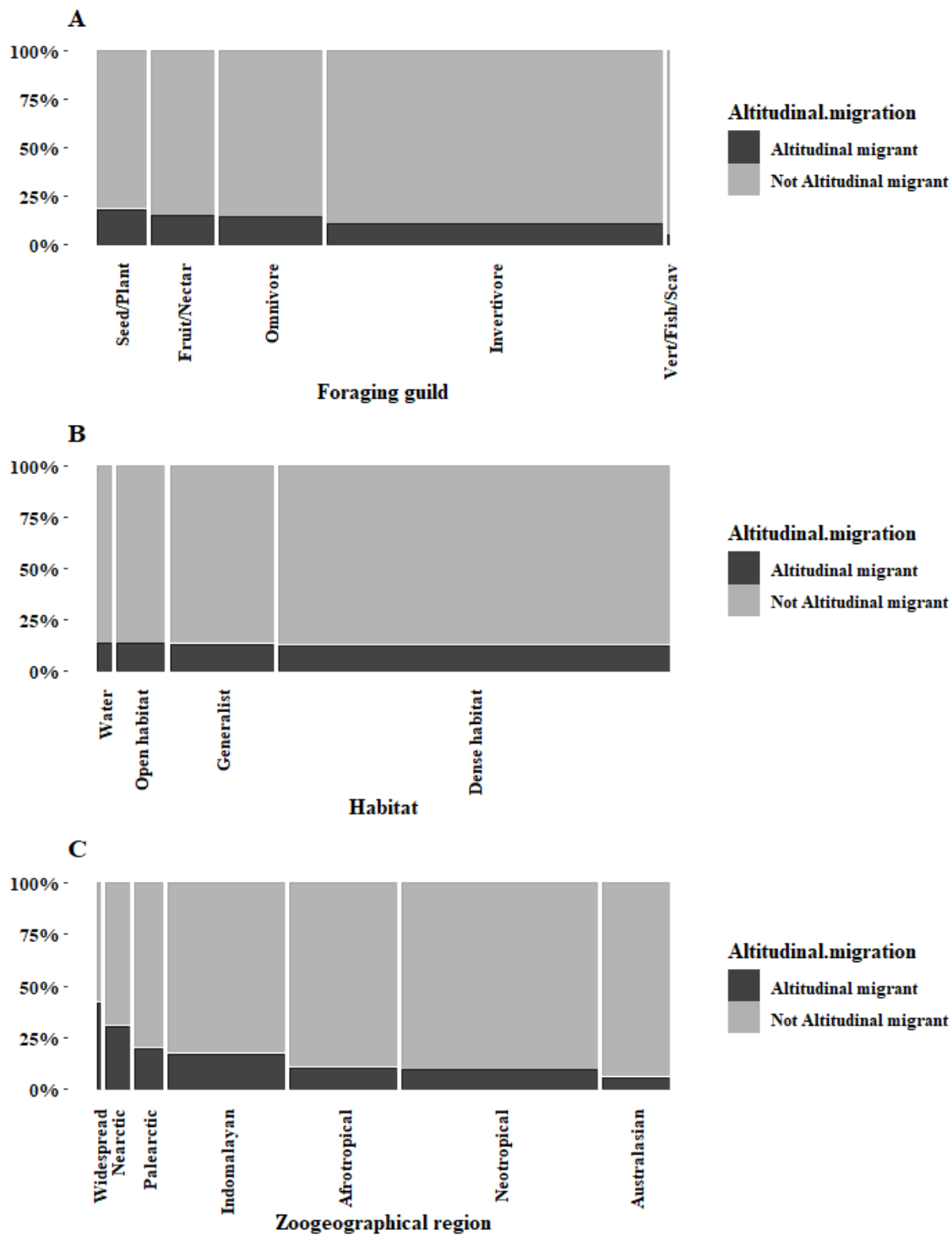
1336

1337 **RESULTS**

1338 The best phylogenetic generalized least square model that predicted altitudinal
 1339 migration included diet, region, and an interaction between diet and region (Table 4.1; Figure
 1340 4.2). The addition of habitat as a predictor did not improve the model's AIC. However,
 1341 habitat was still associated with altitudinal migration ($F_3 = 3.98$, $p = 0.0076$; Figure 4.2B),
 1342 with more altitudinal migrants in open habitat than dense habitat, water, and generalist. When
 1343 we examined the terms in the top-ranked model, we found strong effects of foraging guild
 1344 ($F_2 = 6.48$, $p = 0.0016$; Figure 4.2A), region ($F_6 = 23.77$, $p < 0.0001$; Figure 4.2C), and a
 1345 foraging guild:region interaction ($F_{12} = 10.05$, $p < 0.0001$). The interaction model revealed
 1346 that herbivore/widespread ($t = 4.75$, $p < 0.0001$), omnivore/Palearctic ($t = 3.26$, $p = 0.0011$),
 1347 and omnivore and herbivore/Nearctic ($t = 7.43$, $p < 0.0001$, $t = 4.43$, $p < 0.0001$) species
 1348 were more likely to exhibit altitudinal migration (Table 4.2).

1349 **Table 4.1.** AIC results for each pglS model. The models are ranked from best to worst.

Rank	Model	DF	AIC	ΔAIC
1	Diet + Region + Diet:Region	22	7880.136	0
2	Diet + Habitat + Region	15	7961.286	81.15
3	Diet + Region	12	7975.992	95.856
4	Habitat + Region	11	7980.389	100.253
5	Region	8	7984.467	104.331
6	Diet + Habitat + Diet:Habitat	13	8086.023	205.887
7	Diet	6	8093.052	212.916
8	Diet + Habitat	9	8097.665	217.529
9	Habitat	5	8105.545	225.409



1350

1351 **Figure 4.2.** Mosaic plots representing the proportion of passerine species that are altitudinal
 1352 migrant (black) or not (grey) for each foraging guild (A), habitat (B), and zoogeographical
 1353 region when considering only breeding distribution (C). The width of the bars on the x-axis
 1354 indicates the proportion of species in each category.

1355
1356**Table 4.2.** T-values for each variable included in the top-ranked model Diet + Region + Diet:Region. Bold variables are statistically significant.

	Value	Standard error	t-value	p-value
Intercept	0.077	0.53	0.14	0.88
Omnivore	-0.0082	0.026	-0.32	0.75
Herbivore	0.033	0.031	1.05	0.29
Australasian	0.0091	0.033	0.27	0.78
Indomalayan	0.021	0.026	0.80	0.42
Nearctic	-0.069	0.054	-1.28	0.20
Neotropical	-0.088	0.052	-1.70	0.090
Palaearctic	-0.051	0.035	-1.45	0.15
Widespread	0.32	0.092	3.43	0.0006
Omnivore: Australasian	0.032	0.043	0.74	0.46
Herbivore: Australasian	-0.062	0.051	-1.21	0.22
Omnivore: Indomalayan	-0.040	0.035	-1.16	0.24
Herbivore: Indomalayan	-0.013	0.040	-0.32	0.75
Omnivore: Nearctic	0.40	0.054	7.43	<0.0001
Herbivore: Nearctic	0.27	0.061	4.43	<0.0001
Omnivore: Neotropical	-0.017	0.037	-0.47	0.64
Herbivore: Neotropical	0.054	0.045	1.19	0.23
Omnivore: Palaearctic	0.19	0.058	3.26	0.001
Herbivore: Palaearctic	0.073	0.061	1.20	0.23
Omnivore: Widespread	0.13	0.26	0.50	0.62
Herbivore: Widespread	0.59	0.12	4.75	<0.0001

1357

1358 **DISCUSSION**

1359 We explored two potential drivers of the evolution of altitudinal migration in
1360 passerines by conducting large-scale phylogenetic comparative analyses. Our results indicate
1361 that foraging guild is evolutionarily associated with altitudinal migration, but this relationship
1362 varies across zoogeographic regions. Habitat did not appear to be strongly linked to the
1363 evolution of altitudinal migration.

1364 Globally, species eating fruit/nectar or seed/plant material were more likely to exhibit
1365 altitudinal migration than omnivores and invertivores, despite the fact that most (61%)
1366 passerine birds are insectivorous. This observation follows most of the literature, which
1367 emphasizes that frugivorous altitudinal migrants track fruit and flower abundance seasonally,
1368 particularly in Costa Rica (Blake, & Loiselle, 2000; Boyle et al., 2011) and Nepal (Katuwal
1369 et al., 2016). Note that Barçante et al. (2017), in a study including all bird orders (not only
1370 Passeriformes), showed that invertivorous altitudinal migrants were more abundant around
1371 the world than altitudinal migrants with other type of diet. Indeed, the number of invertivore
1372 species that are altitudinal migrants is higher than that of any other foraging guild; however,
1373 most Passeriformes are invertivore and that foraging guild is by far the most speciose (4018
1374 of 6579 species). However, the proportion of invertivorous altitudinal migrants was relatively
1375 low and we found no evolutionary association between altitudinal migration and invertivory
1376 for passerines, either globally or within regions. Note, however, that the classification of each
1377 species to one foraging guild is tricky because diet can vary through the seasons. Some birds
1378 might rely heavily on insects during the breeding season, but switch to fruits during the non-
1379 breeding season. If food abundance is driving altitudinal migration, such species may
1380 respond to insect abundance during the breeding season and fruit during the non-breeding
1381 season. This situation likely reduced the effect of the patterns that we observed as we only
1382 considered the primary foraging guild (e.g., the main guild for each species depending on the
1383 distribution of the percentage among the diet categories, according to Wilman et al. 2014)

1384 The regions that revealed an evolutionary association between altitudinal migration
1385 and foraging guild were the Nearctic, Palearctic, and Widespread. However, the foraging
1386 guilds associated with altitudinal migration differed between these regions. In the Nearctic,
1387 herbivore and omnivore species were more likely to be altitudinal migrants, a finding
1388 consistent with Boyle (2017). However, it is interesting that omnivorous species appear to be
1389 linked with altitudinal migration. This might support Chaves-Campos (2004) and Levey
1390 (1988), who suggested that birds should follow fruit abundance during the non-breeding
1391 season and insect abundance during the breeding season. Altitudinal migration would then be
1392 beneficial for omnivorous species. Omnivorous species are also linked to altitudinal
1393 migration in the Palearctic. Barçante et al. (2017) indicated that the proportion of
1394 frugivore/nectarivore species that are altitudinal migrant in the Palearctic was lower than

1395 expected; our results demonstrating a disproportionate number of omnivorous species agrees
1396 with their findings. For the species with a widespread distribution, herbivorous species were
1397 associated with altitudinal migration. This finding agrees with previous studies where
1398 herbivorous species have been indicated as altitudinal migrants all around the world (Blake,
1399 & Loiselle, 2000; Guillaumet, Kuntz, Samuel, & Paxton, 2017; Katuwal et al., 2016; Kimura
1400 et al., 2001; but see Barçante et al., 2017). However, only 26 species are considered to have a
1401 widespread breeding distribution, so this interpretation should be taken with caution. For the
1402 other regions (Neotropical, Indomalayan, Afrotropical, and Australasian), foraging guild was
1403 not directly associated with altitudinal migration, potentially due to the vast complexity of
1404 tropical ecosystems.

1405 Habitat was not associated with altitudinal migration in the top model, providing no
1406 additional information beyond what diet and region already provided. The proportion of
1407 altitudinal migrants present in each habitat were extremely similar (12 to 13%); and no
1408 habitat had a disproportionate number of altitudinal migrants. However, habitat was still
1409 significant in the model with habitat only, with open habitats evolutionarily associated with
1410 altitudinal migration. Thus, habitat may have played a role in the evolution of altitudinal
1411 migration, but foraging guild remains the main factor driving it our analysis.

1412 Altitudinal migration is challenging to study in part because of the variability in the
1413 expression of the behaviour. For instance, some populations within the same species are
1414 altitudinal migrants while the others are resident (Boyle 2017; Green, Whitehorne,
1415 Middleton, & Morrissey, 2015; Rabenold, & Rabenold, 1985). There is also variation in the
1416 propensity to engage in altitudinal migration among individuals within a population (Boyle,
1417 2017; Boyle, 2008b; Pratt et al., 2017; Rohwer et al., 2008) and within individuals across
1418 time (Hahn et al., 2004). In addition, most studies focus on the importance of altitudinal
1419 migration to birds moving to reach breeding grounds, but birds may also move up or
1420 downslope to reach moulting grounds (Rohwer et al., 2008; Wiegardt et al., 2017). As such,
1421 this variation makes it extremely difficult to generalize and categorize birds as altitudinal
1422 migrants. We suggest that more studies are needed about specifics of altitudinal migration
1423 encompassing species not yet studied and that these should begin to formalize distinctions
1424 between different types of altitudinal migration (e.g., facultative, breeding, moulting) to

1425 better understand this behaviour and the drivers behind it (sensu Tonra and Reudink, 2018,
1426 formalization of moult-migration). Moulting and breeding are both energetically demanding
1427 and could both lead to strong selection for altitudinal movements. However, there are still
1428 some major differences between moulting and breeding and those differences could be
1429 crucial in explaining the evolution of altitudinal migration.

1430 Another limitation in our study is the lack of information for some regions (Barçante
1431 et al., 2017). We have confidence in the Nearctic since it has been well sampled and
1432 documented; approximately 31% species are altitudinal migrants, which is the highest
1433 proportion within passerines with the exception of Widespread. Otherwise, most studies in
1434 the Neotropics are concentrated in Costa Rica and there is limited research on altitudinal
1435 migration in the Afrotropical, Indomalayan, and Australasian regions (Barçante et al., 2017).
1436 Even the Palearctic, which is rich on research in avifauna, lacks data on altitudinal migration.
1437 This could mean either that altitudinal migration is rare in the Palearctic or that it has not
1438 been studied in depth.

1439 The present study is the first to examine potential large-scale drivers of the evolution
1440 of altitudinal migration in passerines. Altitudinal migration has evolved independently in
1441 different regions of the world under the different environmental pressures coupled with
1442 varying life history characteristics. Our results have reinforced the idea that diet (foraging
1443 guild) played a major role in the evolution of altitudinal migration. However, the relationship
1444 between diet and altitudinal migration is complex and varies across different regions in the
1445 world. Given the prevalence of this behaviour across foraging guilds, diet is clearly not the
1446 only factor that drove the evolution of altitudinal migration, but rather the evolution of this
1447 trait was likely driven by an ensemble of factors.

1448

1449

1450

1451

1452 **LITERATURE CITED**

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CHAPTER 5: CONCLUSION

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1566

1567 The goal of this thesis was to understand the potential drivers behind the evolution of
1568 alternative molting and migration strategies in passerines. Specifically, the evolution of molt-
1569 migration in North America, winter moults in North America and Europe, and altitudinal
1570 migration worldwide. To achieve my goal, I used phylogenetic analyses to correct for the
1571 non-independence among related species. I found that the evolution of molt-migration in
1572 North American passerines was driven by drier breeding grounds at the end of the summer
1573 which push species to migrate somewhere else to replace their feathers. For the evolution of
1574 winter moults, for both European and North American passerines, I found that it was
1575 influenced by the conditions on the overwintering grounds. Specifically, a prebasic moult on
1576 the overwintering grounds was associated with longer day lengths which could increase the
1577 duration of the absorptive state for nutrients essential for moult (Murphy and King 1991;
1578 Renfrew et al. 2011). The presence of a second moult in the annual cycle was also associated
1579 with longer day lengths during the winter for both European and North American passerines;
1580 longer day lengths increase feather wear as a result of UV radiation exposure, hence the need
1581 to replace some feathers a second time. In addition to day length as a driver of the second
1582 moult, open habitats would also play a role in the presence of second moult for European
1583 passerines. Open habitats would increase rapid feather wear by exposing birds to harsher
1584 conditions and more UV radiation, resulting in the need to replace feathers twice. My results
1585 indicated that undergoing two complete moults during the annual cycle was linked to high
1586 primary productivity on the overwintering grounds for European species; having access to an
1587 abundance of resources may reduce the costs associated with a second complete moult.
1588 Finally, the evolution of altitudinal migration was linked to diet, but this relationship varies
1589 across regions. In North America, herbivorous and omnivorous species were associated with
1590 altitudinal migration; in Europe and Asia, omnivorous species were associated with
1591 altitudinal; migration. All these results indicate the importance of environmental conditions
1592 and life history characteristics on the evolution of molt and migration strategies.

1593 The strengths of my research are the use of phylogenetic comparative analysis and the
1594 great number of species included. Indeed, phylogenetic comparative analyses are essential

1595 when studying evolutionary phenomenon because they correct for the non-independence
1596 among species (Ives and Zhu 2006). Otherwise, false correlation can be observed. Related
1597 species often share the same trait because they inherited it from their ancestor and not
1598 because they evolved it independently. It is thus important to consider a particular trait as one
1599 evolutionary event when two related species inherited it from their ancestor. An example of
1600 this are my results from chapter 4; when using phylogenetic analyses, I found a link between
1601 herbivorous and omnivorous species and altitudinal migration. Without the use of a
1602 phylogeny, a link between invertivore species and altitudinal migration is found (Barçante et
1603 al. 2017). This is because the majority of passerines are invertivore and, by consequence, a
1604 higher number of altitudinal migrant species would also be invertivore. With the
1605 phylogenetic analyses, all the closely related species that are invertivores and altitudinal
1606 migrants are considered as only one evolutionary event instead of multiple instances.

1607 The second strength of my research is the great number of species included in the
1608 analyses. Indeed, I analysed all migrant passerines in North America for my first research
1609 chapter, then all migrant passerines in North America and Europe for my second research
1610 chapter, and all passerines worldwide for my last research chapter. Including that many
1611 species lends greater confidence to my results and my interpretation of the evolution of these
1612 strategies.

1613 The downfall of including that many species is that for some species, data are missing
1614 or incomplete. In addition, my analyses fail to account for intraspecific variation that can be
1615 encountered for some species. These problems have been treated in my research by using
1616 different solutions that are not always perfect. For the missing data, we were able to find the
1617 information from other sources or, in rare occasions (noted in the methods), we assumed that
1618 the trait was shared with the closest relative species. When we could not use one of the
1619 previous solutions, we removed the species from the analysis. For the variation within a
1620 species, we normally classified the species as showing the trait of interest or not and did not
1621 account for variation in order to look at broad-scale taxonomic and geographic patterns. It
1622 would be important, for future research, to include the variation among populations and the
1623 presence of plasticity in the trait to see what role it would play in the evolution of molting
1624 and migration strategies.

1625 My thesis highlighted the importance of environmental and life history characteristics
1626 in the evolution of molting and migration strategies derived from the ancestral state.
1627 Moreover, my results clearly indicate how stopover molt locations are essential for many
1628 species of passerines. To effectively conserve species, we need to understand the full annual
1629 cycle (Marra et al. 2015). To do this, we need to understand molting and migration ecology
1630 and not just focus on the breeding part of the annual cycle. In a world of climate change,
1631 understanding the drivers behind molting and migration strategies could help us understand
1632 how species can adapt and which ones will be more resilient to ongoing environmental
1633 change.

1634 The next steps in the study of molting and migration strategies would be to focus
1635 research efforts on identifying the strategies use by species with missing data; this is
1636 particularly the case of certain regions such as Afrotropical, Indomalayan, and Australasian
1637 regions for the migration strategies (Barçante et al. 2017) and molt strategies of birds outside
1638 Europe and north America. It would also be interesting to look at the plasticity of molt and
1639 migration and how the strategies vary among populations. Finally, since my research only
1640 focused on passerines, it would be relevant to see if other orders of birds are also driven by
1641 the same factors in the evolution of their molt and migration strategies.

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1651 **LITERATURE CITED**

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