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Evolutionary biology

Evolution of moult-migration is directly linked to aridity of the breeding grounds in North American passerines

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

1. Background

Feathers are unique to birds and are critical to nearly every aspect of their biology, including flight, thermoregulation and visual communication [1]. Each year, birds must exchange old feathers for fresh ones by moulting [2,3]. An energetically expensive stage of the annual cycle [4–8], moulting requires specific resources to produce high-quality feathers. Hence, the timing and location of moult are crucial for the production of feathers of sufficient quality to maximize lifetime reproductive success [9]. To avoid energy allocation conflicts, birds generally separate the most energetically expensive life-history events during the annual cycle: breeding, migration and moult [10]. Most migratory passerines complete their moult on the breeding grounds prior to autumn migration. However, some have evolved a moult-migration strategy, the 'temporal overlap in the moult and migration life-history stages' [11].

Moving to a stopover location i.e. a rest/refueling site during migration [12], to moult (stopover moult-migration [11]) or moulting during migration (continuous moult-migration [11]) must confer benefits that outweigh the costs of overlapping these two energetically demanding life-history stages. One advantage to continuous moult-migration could be reducing the overall time used for these events, thus advancing arrival date at stationary non-breeding grounds, which might provide various advantages (see below). For stopover moult-migration, an advantage might be the ability to acquire high-quality resources to support moulting. For example, various species breeding in western North America moult in the monsoon region of northwestern Mexico and southwestern

USA [13,14]. Here, the late-summer monsoon rains result in an explosion of productivity that may 'pull' species to this area to take advantage of abundant resources [14,15].

While the richness of the Mexican monsoon region may 'pull' moult–migrants to stopover, other factors may also 'push' them to depart prior to moult, including aridity of the breeding grounds at the end of the summer or a time constraint at high latitudes. The combination of good conditions at stopover locations with unfavourable conditions on the breeding grounds during the post-breeding period forms the push–pull hypothesis. This hypothesis has often been proposed as an explanation for the evolution of stopover moult-migration in the Mexican monsoon region [14,16,17], but has not yet been empirically tested.

Several drivers of moult-migration evolution have been hypothesized, such as migration distance, aridity of the breeding grounds during the post-breeding period, winter territoriality, length of the breeding season and number of broods produced during the breeding season. Long migration distances and a long breeding season, especially if raising multiple broods, may reduce the time available between the end of breeding and start of migration and not allow for the replacement of all feathers [18–21]. Arid breeding grounds could select for moult-migration because the lack of resources at the end of summer in western North America limits the ability to grow feathers of sufficient quality [14,22]. Finally, moult-migration might be favoured in species that defend non-breeding territories because it would allow earlier arrival at the non-breeding grounds, and thus the acquisition of higher quality territories [23,24].

Revealing the mechanisms responsible for the evolution of overlapping life-history stages is critical to understanding the dynamics of migratory bird populations and how they are limited. Migration places enormous phenological constraints on avian life histories, the organization of which is shaped by both biotic and abiotic factors [10]. Environmental changes, including land-use and global climate alterations, are shifting the availability of resources both spatially and temporally, potentially altering the playing field of selection [e.g. 25]. Understanding the factors that drive the organization of annual cycles will help us predict the resilience of species to environmental change, as well as identify species in need of proactive management [26].

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

2. Methods

(a) Data collection

We collected data for 200 species and five subspecies of migratory passerines breeding in Canada and/or the USA (electronic supplementary material, table S1). Three species (*Vireo gilvus*, *Haemorhous purpureus* and *Passerina ciris*) were divided into their Eastern and Western subspecies or populations, which differ in moult strategy, for a total of 208 taxa. We classified species with respect to where they can undergo prebasic moult (i.e. complete moult resulting in the basic plumage [4]): breeding, wintering grounds or during migration. We followed Tonra and Reudink's [11] classification to specify which category of moult-migration (stopover, continuous or suspended) the species conformed to. To determine prebasic moulting strategy, we used descriptions of moulting from Birds of North America species accounts [27], Pyle [28] and the literature [13,14,29–33]. When variation in moulting strategy among individuals of the same species was encountered, we classified that species as a moult–migrant. Altitudinal migrants (six species) were categorized as moulting on their breeding grounds.

(b) Potential drivers of moult-migration

Migration distance was approximated as the distance (Mm) from the centroid of the breeding distribution to the centroid of the non-breeding distribution. Distribution maps from Birdlife International [34] were used in the calculation of NDVI. NDVI is a measure of live green vegetation and was used to indicate the aridity of the breeding grounds during the post-breeding period in North America (1 July–31 August). Winter territoriality category (yes or no) was taken from Birds of North America [27]. Data on the number of broods were retrieved from Birds of North America [27]. This predictor was categorical: one or multiple broods. More information on how the predictors were retrieved is available in the electronic supplementary material.

(c) Phylogeny

Using BirdTree.org [35], we downloaded 1000 possible trees of a phylogeny subset containing our 200 species of passerines from 'Hackett All Species: a set of 10 000 trees with 9993 OTUs each' [36]. Using TreeAnnotator v. 1.10.4 [37], we then created a maximum clade credibility tree with our 1000 trees using 1% burn-in (as states) and mean heights for node heights. We added the eight subspecies in R [38] to obtain a maximum clade credibility tree of 208 species and subspecies, which we used for all our analysis. The visual representation of our phylogeny (figure 1) was created using the *phytools* package of R [39].

(d) Statistical analysis

We used phylogenetically controlled analysis to investigate factors associated with the evolution of moult-migration (including stopover, suspended and continuous moult; 45 species) and specifically the stopover moult-migration strategy (13 species) for which the push–pull hypothesis was originally devised. Note, however, that we could only test the 'push' aspect of the hypothesis because moulting distributions are unavailable. In both (stopover or moult-migration), the response variables were binary, with 1 indicating presence of stopover or moult-migration and 0 indicating absence. We then used phylogenetic logistic linear models to test the predictors by creating a full model that included all explanatory variables (NDVI, migration distance, number of broods and winter territoriality) and sequentially eliminated non-significant variables ($p > 0.05$) to arrive at a final best fit model. No explanatory variables were highly correlated (all $r < 0.31$). Analyses were conducted in R [38] using the package phyloglm [40]. The 'logistic_MPLE' method was applied with a btol of 10, a log.alpha.bound of 10, and no bootstrap.

3. Results

When we examined the factors associated with moult-migration, both NDVI ($z = -2.72$, $p = 0.006$) and migration distance ($z = 2.68$, $p = 0.007$) were retained in the final model, indicating that moult–migrants were more likely to migrate longer distances and have

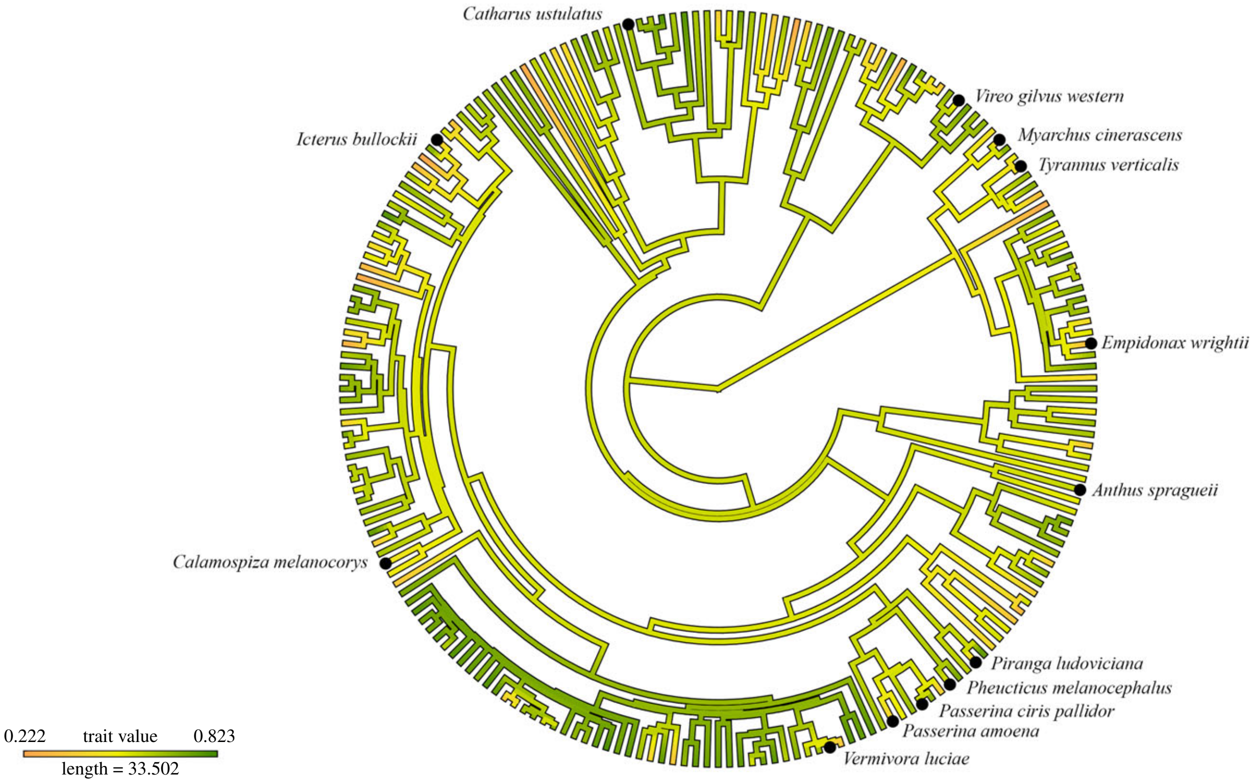

Figure 1. Phylogeny of the 208 species of North American migrant passerines. The colour of the branches represents the average NDVI of the breeding grounds in July and August for each passerine: green indicates high NDVI values and tan low values. The black circles indicate species that are stopover moult–migrants; these are labelled with the scientific name of these species.

Table 1. Predictors of stopover and moult-migration included in the best model of the phylogenetic logistic regression following a stepwise regression (backward elimination). Stopover = stopover moult-migration strategy only ($n = 13$ species), moult-migration = stopover, continuous and suspended moult-migration combined ($n = 45$ species).

	coefficient	estimate	s.e.	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

breeding ranges that are drier in the post-breeding period than non-moult–migrants. Next, we specifically examined the stopover moult-migration strategy. In this case, only NDVI of the breeding range was included in the final model and was strongly negatively associated with stopover ($z = -3.49$, $p = 0.0005$), indicating that the breeding areas of stopover moult–migrants were drier during the post-breeding period than those of non-moult–migrants (table 1).

4. Discussion

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

Aridity has long been proposed as a driver of moult-migration; however, explicit tests of this hypothesis have been lacking. Rohwer *et al.* [14] and Young [22] raised the idea that arid breeding grounds may offer insufficient resources at the end of the summer to grow high-quality feathers, which are essential for flight performance during autumn migration. Substantial energy is required to synthesize new feathers [6–8], thus having an abundance of high-quality resources during moulting is critical. Limitation of resources at the end of the summer would act as a ‘push’ towards moult-migration in North America, particularly in the West, where lowlands become dry and unproductive (figure 2; [22]) at this time. The Mexican monsoon region in northwestern Mexico and

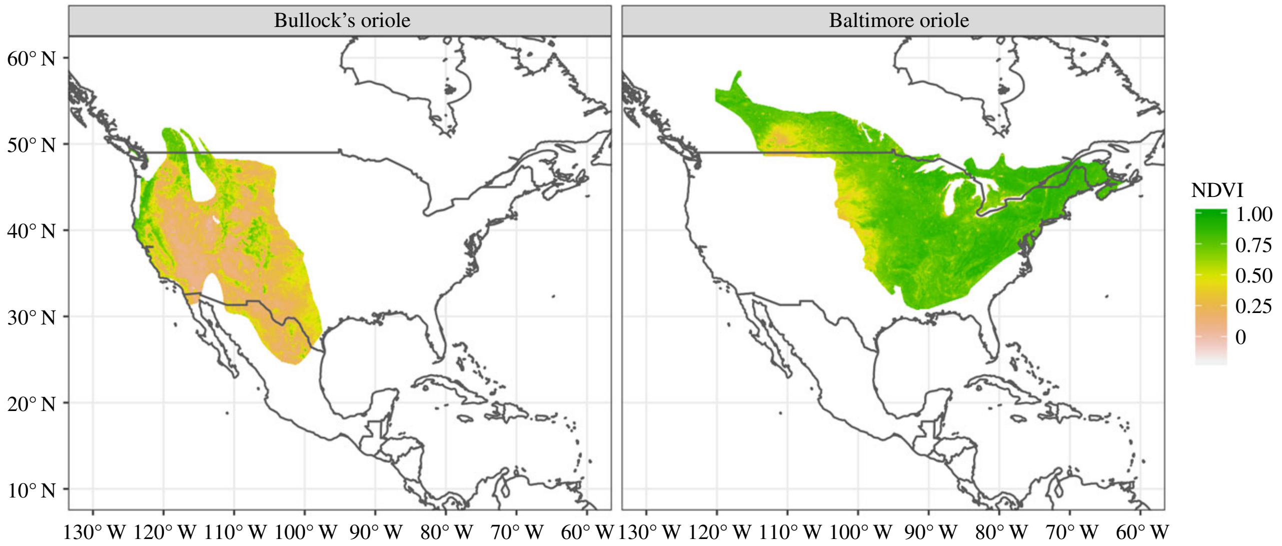

Figure 2. Distribution maps representing NDVI of the breeding grounds (1 July to 31 August) of two North American passerines. Higher values indicate a greater abundance of live green vegetation. *Icterus galbula* (Baltimore orioles) moult on their breeding grounds and their NDVI average is 0.83. *Icterus bullockii* (Bullocks orioles) are stopover moult–migrants and their NDVI average is 0.35.

southwestern USA is an important stopover location to undergo moult for migrant passerines [41] such as *Icterus bullockii* [42], *Tyrannus verticalis* [17] and *Piranga ludoviciana* [32]. Monsoon rains in this region in July and August result in an explosion of resources available for migrant passerines on their way to the non-breeding grounds [43]. An attraction to the Mexican monsoon region, combined with the aridity of the breeding grounds at the end of the summer, likely drove the evolution of some western North American migrant passerines toward stopover moult-migration.

For the alternative factors tested, only migration distance was associated with moult-migration; winter territoriality and number of broods were not present in the best models. As expected, longer migration distances were associated with moult-migration: by imposing a time constraint, they would force moult outside of the breeding grounds [18,19]. This result is in accordance with previous European studies on Sylviidae [19] and Western Palearctic passerines [44] that indicated longer migration distance as a driver of moulting strategies differing from the ancestral state (moult on the breeding grounds) [3]. A time constraint was also the reason behind number of broods as a predictor, but our results suggest this variable was not important in the evolution of moult-migration. Winter territoriality was hypothesized as driving moult-migration and winter moult by Pérez & Hobson [24] and Lindström *et al.* [23], but our results concur with Rohwer *et al.* [14], who did not support the winter territoriality hypothesis [23,24].

Our research examined 208 North American migrant passerines and classified each species as moult–migrant or not. While some species have extensive data and were easy to fit into a category (e.g. *I. bullockii* [42]), those exhibiting intra-specific variation in moulting strategy were more challenging. In addition, Pyle *et al.* [28] described a wide variety of post-breeding dispersal movements for moulting in many passerines. These dispersal movements might be a type of moult-migration; however, we took a conservative approach in our analysis and did not account for these movements since they do not fit the definition of moult-migration provided by Tonra and Reudink [11]. Intra-specific variation also exists for the explanatory variables (migration distance, winter territoriality, number of broods): thus, these categorizations at the species level are purposely rough in an effort to describe broad-scale taxonomic and geographic patterns, and a more detailed and nuanced study that accounted for that variation at the individual level would be useful for future research.

Our results strongly support the 'push' aspect of the push–pull hypothesis proposed by Rohwer *et al.* [14]; arid breeding grounds during the post-breeding period 'push' some migrant passerines towards a stopover moult-migration strategy that capitalizes on the abundant resources available in the Mexican monsoon region during late-summer and early autumn. However, to fully understand push–pull dynamics, future studies should explore the 'pull' aspect of the hypothesis. Our results also indicate that migration distance played a role in the evolution of moult-migration. Understanding such environmental drivers in species' ecology is critical at this time, particularly for the chronically understudied portions of the annual cycle outside of breeding [26]. Given contemporary conservation challenges, such as climate and land-use change, this study raises the question: how plastic are species in their ability to adopt or cease a moult-migration strategy should aridity increase or decrease in their breeding range? [25]. In addition, how could changing climatic conditions alter the relative strength of the 'push' and/or 'pull' of breeding and moulting grounds, respectively? The answer to these questions could reveal which species will be most resilient to ongoing environmental change.

Data accessibility. Data and code are accessible from Dryad (https://doi.org/10.5061/dryad.vhhmgqnqq) [45].

Authors' contributions. C.P. collected the data, performed phylogenetic analyses, analysed output data and wrote the manuscript. M.W.R. conceptualized and supervised the project, and edited the manuscript. C.M.T. and N.J.F. helped with literature, classification of moult-migration, and editing. C.M.T. also contributed to writing. M.S. provided statistical support for phylogenetic analyses. All authors contributed substantially to revisions. All authors approved the final version of the manuscript and agree to be held accountable for the content.

Competing interests. We declare we have no competing interests.

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