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# Evolution of seasonal ecological niches in the *Passerina* buntings (Aves: Cardinalidae)

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The evolution of migration has long been considered complex and recent work has demonstrated additional complexity: some species follow the same ecological conditions throughout the year, whereas others 'switch niches' between breeding and wintering ranges. Hypotheses regarding the evolution of migration would generally predict niche-following as primitive, and niche-switching as derived. However, no test has, to our knowledge, yet determined the directionality of evolution of these states within a lineage. We present an analysis of phylogenetic dimensions of seasonal niches in the *Passerina* buntings that indicates greater evolutionary change in the niches of breeding populations than among those of wintering populations. These results are consistent with hypotheses of (i) niche conservatism (in winter, at least) across a recently speciated lineage; and (ii) the derived state of the breeding (rather than winter) ecological niches of each species.

**Keywords:** migration; *Passerina*; phylogeny; ecological niche modelling

## 1. INTRODUCTION

A fascinating feature of several biological systems is the phenomenon of seasonal migrations. Although this phenomenon has long attracted researchers (Rappole 1995; Berthold 2001), many aspects of its evolution remain poorly known. In particular, as pointed out recently by Zink (2002; but see a rebuttal by Rappole *et al.* (2003)), studies of migratory behaviour have not viewed the evolution of migratory systems in a historical context, and can thus offer only indirect insights into their evolutionary history.

Ecological niches can be defined as the suite of conditions within which a species can maintain populations without immigrational input (Grinnell 1917, 1924; MacArthur 1972), and they thus constitute an important constraint in species' distributional biology. Theoretical studies of the evolution of ecological characteristics predict that it will generally be conservative, with innovation occurring only under restrictive circumstances (Bradshaw 1991; Brown & Pavlovic 1992; Kawecki & Stearns 1993; Kawecki 1995; Holt 1996; Holt & Gomulkiewicz 1996). Recent studies of ecological niche characteristics in evolving lineages have confirmed this prediction across a variety of taxa and time-scales, including: (i) in newly founded populations of invasive species (Peterson & Vieglais 2001); (ii) across the Pleistocene–Recent transition (i.e. 21 000 yr BP to the present; Martínez-Meyer 2002); (iii) between sister species pairs (Huntley *et al.* 1989; Ricklefs & Latham 1992; Peterson *et al.* 1999); and (iv) across phylogenies of species groups (Martínez-Meyer 2002). Overall, the picture is one of ecological niches as

a long-term stable constraint on the distributional potential of species.

A few studies have begun to explore the idea that this niche conservatism applies across seasonal shifts in distributions as a part of migratory systems. In particular, recent studies of New World austral migratory birds revealed patterns suggestive of some species being 'niche followers' (i.e. using the same climatic niche year-round) and others being 'niche switchers' (i.e. changing niches between seasons) (Joseph 1996, 2003; Joseph & Stockwell 2000). A broader review focusing on nearctic–neotropical migrant species (Nakazawa *et al.* 2004) confirmed this dichotomy: many species (*ca.* 28.6% of species examined) effectively switch niches qualitatively from one season to the other. This latter study, as well as theory regarding the evolution of migratory systems (Gauthreaux 1982; Berthold 1988, 2001; Levey & Stiles 1992; Rappole 1995; Chesser & Levey 1998), suggests that niche-following would be the plesiomorphic state, and that niche-switching would be the apomorphic state. No phylogenetic hypothesis was available for the taxa examined by Nakazawa *et al.* (2004), preventing a test of this hypothesis.

The *Passerina* buntings probably evolved from a Mesoamerican ancestor, given the present distribution of species richness in the genus, their sister-group relationship with the neotropical *Cyanocompsa* (Klicka *et al.* 2001) and the lack of close relatives elsewhere in the Holarctic. Current theory regarding the evolution of migratory behaviour in such groups (Gauthreaux 1982; Berthold 1988, 2001; Levey & Stiles 1992; Rappole 1995; Chesser & Levey 1998) generally paints a stepwise scenario of (i) original Mesoamerican distribution; (ii) local tracking of resources; (iii) longer-distance resource tracking; and (iv) 'hard-wiring' this tracking into predictable migratory movements northward to breeding distributional areas. Hence, a clear prediction is that winter

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ecological niches would be expected to be more similar to ancestral conditions than breeding ecological niches.

In this contribution, we develop detailed phylogenetic tests regarding the evolution of components of migratory behaviour in the *Passerina* buntings, for which a detailed phylogeny based on molecular characteristics has already been developed (Klicka *et al.* 2001). Initial studies of this phenomenon (Joseph & Stockwell 2000; Joseph 2003) and our initial survey of seasonal niches (Nakazawa *et al.* 2004) have focused on groups for which reliable phylogenetic information was largely unavailable. The *Passerina* buntings, however, present a rare combination of: (i) including both migratory and non-migratory species; (ii) among migratory forms, including both niche-switchers and niche-followers; and (iii) a phylogenetic hypothesis (Klicka *et al.* 2001). Our results strongly support the idea that niche-switching and distinct breeding niches represent derived states, a 'next level' of complexity in the evolution of migratory systems.

## 2. METHODS

Ecological niches of species were modelled using the genetic algorithm for rule-set prediction (GARP) (Stockwell & Noble 1992; Stockwell 1999; Stockwell & Peters 1999; see http://www.lifemapper.org/desktopgarp/). GARP is an evolutionary computing application that seeks non-random associations between point-occurrence data and ecological information in the form of electronic maps, in an iterative process of random rule generation, evaluation, perturbation, testing and incorporation or rejection. The resulting models identify portions of ecological space that reflect niche dimensions that are sufficiently relevant to yield statistically robust representations of the geographical distributions of species: it should, of course, be borne in mind that these models are correlative, and that niches almost certainly vary in other ecological dimensions that are not included in the present study. The approach has been described in detail elsewhere (Stockwell & Noble 1992; Stockwell 1999; Stockwell & Peters 1999; Peterson *et al.* 2002).

Point-occurrence data for *Passerina* buntings were obtained from a variety of sources: North American Breeding Bird Survey database (http://www.mp2-pwrc.usgs.gov/bbs/), Christmas Bird Count (http://www.audubon.org/bird/cbc/) and from the Atlas of the Mexican Bird Distributions (Peterson *et al.* 1998; Navarro-Sigüenza *et al.* 2002), a compendium of label data compiled from natural history museum specimens of birds from Mexico (see acknowledgments). As no point-occurrence information was readily available for South America and the Caribbean, we limit our analyses to North America and northern South America.

Ecological data layers included 12 parameters (maximum, minimum and mean temperature; diurnal temperature range; ground frost frequency; solar radiation; precipitation; vapour pressure; wet-day frequency; elevation; slope; and aspect). Climatic variables were interpolated from weather station data for 1961–1990 and resampled to 30′ resolution (New *et al.* 1997) (http://ipcc-ddc.cru.uea.ac.uk/). Topographic data were obtained from the US Geological Survey (http://edcdaac.usgs.gov/gtopo30/hydro/) at a spatial resolution of 1 km². All variables were resampled to 0.1° spatial resolution (equivalent to *ca.* 10 km). The region for analysis was limited to the approximate union of the geographical distribution of point occurrences

in our dataset for all species involved: southern Canada south to northern South America.

Three environmental datasets were prepared for analyses, permitting us to model ecological niches on breeding and wintering distributional areas for migratory species, or on year-round distributional areas for resident species: (i) 'annual', using annual mean values of climatic variables; (ii) 'breeding', using mean values across April–June (when most migratory forms are establishing territories and breeding (Lanyon & Thompson 1986; Payne 1992; Greene *et al.* 1996; Groschupf & Thompson 1998; Lowther *et al.* 1999)); and (iii) the 'winter' set, using mean values across December–February. Occurrences of the five migratory species (*Passerina amoena*, *P. ciris*, *P. cyanea*, *P. versicolor* and *P. caerulea*) were divided into breeding and wintering datasets (data from other months were discarded) and analysed with the respective seasonal ecological datasets; year-round occurrences were used in combination with the 'annual' dataset for the four resident species (*P. leclancherii*, *P. rositae*, *Cyanocompsa cyanoides* and *C. parellina*). Thus, 14 entities (species or species × season) were analysed; ecological niche models were developed for each, and projected onto all three seasonal ecological datasets (i.e. for resident species, annual data were used to build ecological niche models that were projected onto annual, breeding and winter datasets; for migratory species, winter data were used to build ecological niche models that were projected onto annual, breeding and winter datasets; and breeding data were used to build ecological niche models that were projected onto annual, breeding and winter datasets).

To optimize model quality, we developed 100 replicate models for each entity based on random 50–50 splits of available occurrence points; out of these models, we selected the 10 'best', following Anderson *et al.* (2003). This procedure is based on the observations that (i) models vary in quality; (ii) variation among models involves an inverse relationship between errors of omission (leaving out true distributional area) and errors of commission (including areas not actually inhabited); and (iii) best models (as judged by experts blind to error statistics) are clustered in a region of minimum omission of independent test points and moderate area predicted present (an axis related directly to commission error). The position of a particular model in relation to the two error axes provides an assessment of the relative accuracy of each model. To choose best subsets of models, we (i) eliminated all models that had greater than 5% omission error based on independent test points; (ii) calculated the median area predicted present among these low-omission points; and (iii) identified models within 1% of the overall median area predicted present.

Ecological similarity among entities was assessed via interpredictivity calculations (Peterson *et al.* 1999; Martínez-Meyer 2002), which take advantage of the observation that species seldom inhabit the entire spatial extent of their niches (Peterson *et al.* 1999; Peterson & Vieglais 2001), with niches reflecting the overall extent of potentially habitable conditions. This approach involved (i) the projection of models for one species or species × season onto environmental datasets for the other seasons or for the entire year; and (ii) the overlay of locality records for all other species or species × seasons. Niche similarity was measured as the percentage of points of entity A falling within the prediction area of the model of entity B, and vice versa (Peterson & Vieglais 2001). In this way, we built an interpredictivity matrix in which columns represent models predicting and rows the percentage of occurrences predicted correctly

Table 1. Summary of interpredictivity analyses in the form of a similarity matrix, showing the ability of each ecological niche model (columns) to predict the occurrence points of each species (rows).

(A value of unity indicates a correct prediction of presence for all test points, whereas a value of zero indicates no successful prediction of test points. Numbers are given as proportions of available points. Boxes indicate comparisons among seasons within species. PV, *Passerina versicolor*; PR, *P. rositae*; PL, *P. leclancherii*; PY, *P. cyanea*; PI, *P. ciris*; PA, *P. amoena*; PC, *P. caerulea*; CC, *Cyanocompsa cyanea*; CP, *C. passerina*; W, winter; S, breeding. Comparisons that are statistically significantly ($p < 0.05$) better than random expectations are indicated in bold.)

| | PV-W | PV-S | PR | PL | PY-W | PY-S | PI-W | PI-S | PA-W | PA-S | PC-W | PC-S | CC | CP |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PV-W | **0.945** | **0.492** | 0.000 | 0.000 | **0.969** | 0.000 | **0.953** | 0.000 | **0.859** | **0.422** | **0.969** | **0.117** | 0.000 | 0.063 |
| PV-S | **0.516** | **0.961** | 0.000 | **0.405** | **0.974** | **0.118** | **0.980** | **0.399** | 0.059 | 0.294 | **0.948** | **0.706** | **0.111** | **0.471** |
| PR | **0.250** | **0.975** | **1.000** | **0.975** | **1.000** | 0.000 | **1.000** | **0.250** | 0.025 | 0.000 | **1.000** | **0.525** | **0.375** | **0.975** |
| PL | 0.226 | **0.887** | **0.758** | **0.952** | **0.960** | **0.129** | **0.992** | **0.476** | 0.032 | 0.008 | **0.992** | **0.685** | **0.355** | **0.960** |
| PY-W | **0.388** | **0.231** | 0.000 | 0.007 | **0.937** | 0.000 | **0.794** | 0.003 | **0.444** | **0.140** | **0.836** | 0.066 | 0.035 | **0.080** |
| PY-S | 0.006 | 0.182 | 0.000 | 0.047 | **0.974** | **0.910** | **0.688** | **0.282** | **0.408** | 0.035 | **0.972** | **0.716** | **0.318** | **0.218** |
| PI-W | **0.527** | **0.273** | 0.000 | 0.000 | **0.977** | 0.000 | **0.936** | **0.009** | **0.495** | **0.091** | **0.945** | **0.086** | **0.041** | **0.095** |
| PI-S | **0.119** | **0.847** | 0.000 | **0.389** | **1.000** | **0.728** | **0.998** | **0.938** | 0.060 | 0.038 | **0.998** | **0.986** | **0.709** | **0.804** |
| PA-W | **0.556** | **0.286** | 0.000 | 0.000 | **0.968** | 0.000 | **0.746** | 0.000 | **0.937** | **0.413** | **0.968** | 0.032 | 0.000 | 0.048 |
| PA-S | 0.059 | 0.036 | 0.000 | 0.001 | 0.738 | 0.088 | 0.276 | 0.004 | 0.307 | **0.871** | 0.718 | 0.247 | 0.001 | 0.001 |
| PC-W | **0.546** | **0.260** | 0.000 | 0.000 | **0.959** | 0.000 | **0.847** | 0.000 | **0.633** | **0.296** | **0.939** | **0.077** | 0.015 | 0.066 |
| PC-S | 0.073 | **0.402** | 0.000 | **0.127** | **0.946** | **0.716** | **0.844** | **0.461** | 0.239 | 0.212 | **0.919** | **0.915** | **0.467** | **0.387** |
| CC | 0.000 | 0.175 | 0.143 | 0.159 | **0.984** | 0.032 | **0.984** | 0.127 | 0.095 | 0.016 | **1.000** | 0.238 | **0.937** | **0.905** |
| CP | **0.240** | **0.620** | 0.298 | **0.520** | **0.982** | 0.111 | **0.971** | 0.263 | 0.140 | 0.029 | **0.982** | **0.561** | **0.550** | **0.819** |
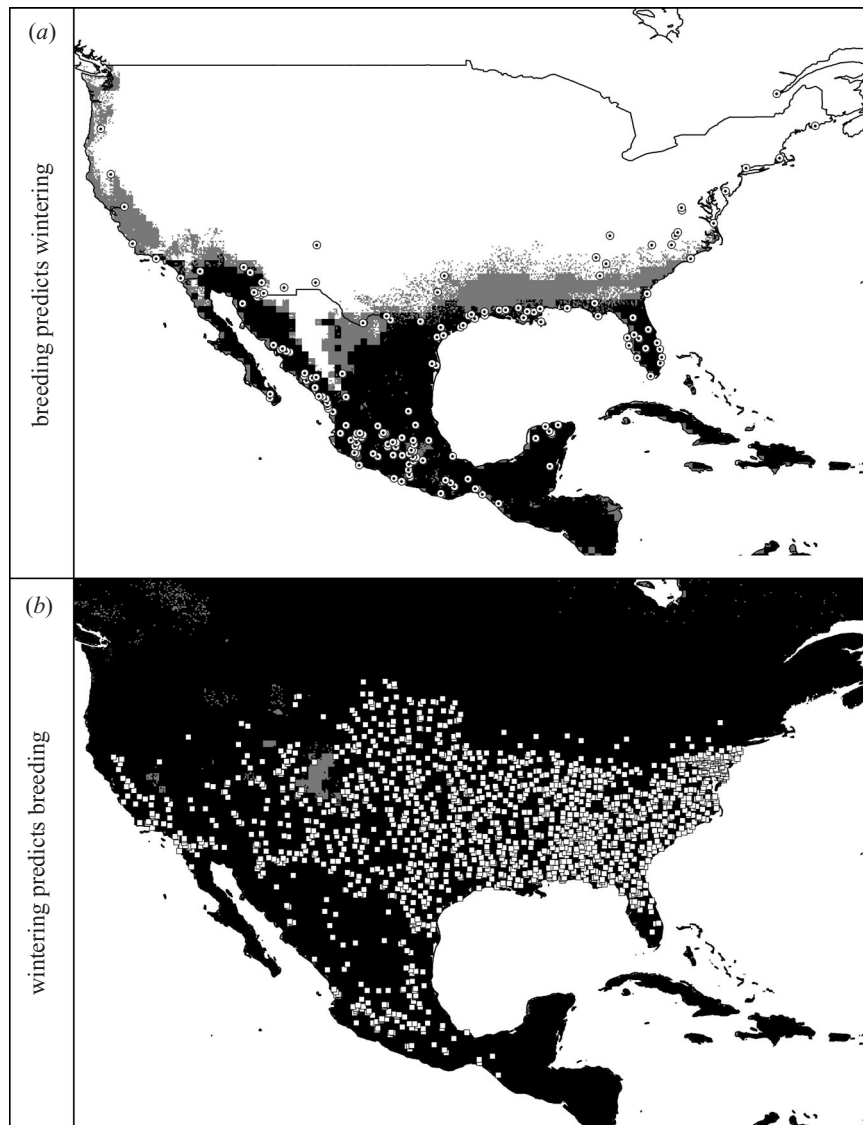
Figure 1. Example of predictions among seasons for *Passerina caerulea*, in which (*a*) distributional occurrences in the breeding season (not shown) are used to build an ecological niche model that is used to predict wintering occurrences (dotted circles), and (*b*) distributional occurrences in the winter are used to build an ecological niche model that is used to predict breeding distributional occurrences (open squares). Darker shading indicates greater coincidence among best-subsets models (white, no model predicts presence; grey, less than 50% of models predict presence; black, a majority of models predicts presence). Note the asymmetry of predictivity among seasons: there is excellent prediction of winter distribution from the breeding ecological niche, but rather poor prediction of breeding distribution from the winter ecological niche; these differences are reflected directly in the asymmetric values in the ecological similarity matrix in table 1.

(Martínez-Meyer 2002). This similarity matrix was transformed into a distance matrix by subtraction of all values from unity.

The ecological distance matrix was analysed in two ways: (i) $\chi^2$ analyses to establish the significance of reciprocal predictions between entities; and (ii) a branch-length fitting procedure for phylogenetic trees. Regarding statistical significance, we first detected pairwise interpredictions that were more successful than random expectations. We compared observed predictive success and failure with that expected based on random association between prediction and test points: the proportion of the study area predicted present or absent by the model × number of test points yielded the random expectations (Peterson 2001; Peterson & Vieglais 2001). Observed and expected numbers were compared using a $\chi^2$ test with one degree of freedom. Pairwise *t*-tests were used to assess whether the interpredictivity among niches modelled based on one season was higher or lower than that among niches modelled based on the other season.

Second, we analysed the ecological distance matrix based on the phylogenetic results of Klicka *et al.* (2001), which were based on sequences of the entire mitochondrial cytochrome *b* gene (more than 1.1 kb). This tree is based on diverse analyses including maximum-parsimony, maximum-likelihood and minimum-evolution approaches. Although some of the nodes in this hypothesis are somewhat weakly supported, this group nevertheless remains one of very few (Joseph *et al.* 1999, 2003, 2004) that shows diverse migratory systems and for which a molecular phylogeny is available. We used fig. 3 from Klicka *et al.* (2001) as the basis for our phylogenetic analyses.

Fitch analyses in PHYLIP (http://bioweb.pasteur.fr/seqanal/phylogeny/phylip-uk.html) (Felsenstein 1993) were used to fit branch lengths representing evolutionary distances in ecological niche characteristics to a user-defined tree structure, while minimizing the deviation from the original input distance matrix (Rice *et al.* 2003). We used the user-determined tree option of
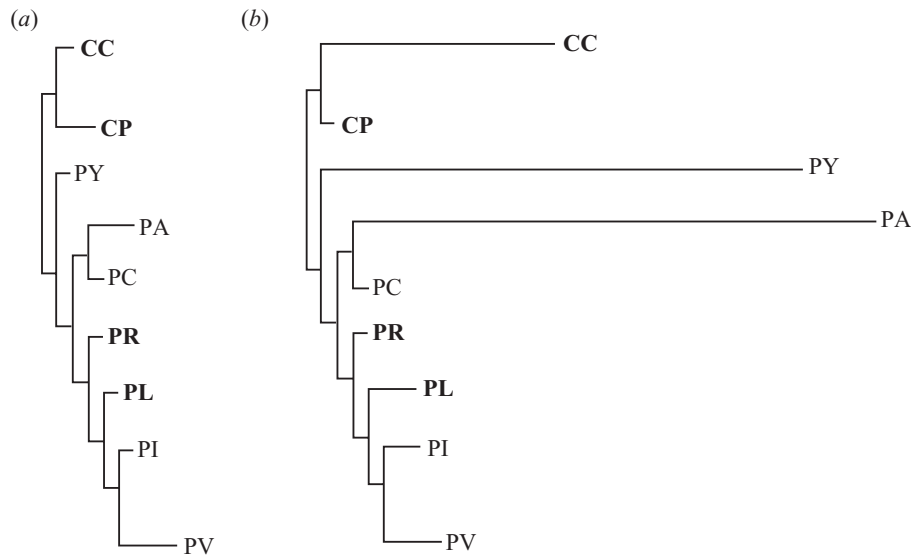
Figure 2. A phylogenetic tree for *Passerina* based on previous molecular studies (Klicka *et al.* 2001), with fitted branch lengths reflecting modelled amounts of evolutionary change in seasonal ecological niches ((*a*) winter versus (*b*) summer) along each lineage. Taxa indicated in bold are resident species. PV, *Passerina versicolor*; PR, *P. rositae*; PL, *P. leclancherii*; PY, *P. cyanea*; PI, *P. ciris*; PA, *P. amoena*; PC, *Passerina caerulea*; CC, *Cyanocompsa cyanoides*; CP, *C. parellina*.

Fitch to set the phylogenetic framework, and estimated branch lengths based on ecological distance matrices to visualize degrees of ecological differentiation in each lineage. These branch lengths can be taken as a measure of evolutionary change in ecological niche characteristics along each branch in the tree. Branch lengths were obtained for the breeding and annual entities as one set, and for the winter and annual entities as another set. A pairwise *t*-test comparing individual estimated branch lengths between the two analyses was used to compare amounts of evolutionary change between seasonal niches.

## 3. RESULTS

Ecological niche models for each species and season were highly predictive of the distribution of the species in that season: models were significantly representative of the ecological niches of each species in each season. In this sense, all models for a particular species in a particular season were able to predict independent subsets of available occurrence data for the same species and season with statistical significance (all $p < 10^{-12}$). This result indicates that models for each species held significant predictive power for distributional phenomena related to that species.

Projections of models among seasons and species indicated variable predictive power, indicative of conservation or differentiation of niche characteristics (table 1). In several cases, prediction of one seasonal distribution of a species from the other was excellent, at much better than null expectations, whereas the converse prediction was poor (e.g. figure 1). In particular, for *P. cyanea*, *P. ciris* and *P. caerulea*, modelled winter ecological niches predicted more than 90% of breeding points, but modelled breeding ecological niches in no case predicted any better than 8% of wintering points (table 1). Predictive ability among species also varied considerably. In general, predictive ability of winter niche models significantly exceeded that of breeding niche models (paired *t*-test: $p < 0.05$).

Modelling the evolution of the niche distances based on the phylogeny indicated generally conservative and gradual ecological niche evolution in winter niches (figure 2). However, patterns of ecological niche evolution in breeding niches are strikingly different, with dramatic change reconstructed for *P. amoena* and *P. cyanea*. Overall, total reconstructed evolutionary change in ecological characters was greater among breeding niches than among winter niches (paired *t*-test comparing branch lengths from each season: $p < 0.05$), suggesting greater divergence of breeding niche characteristics than of winter niche characteristics.

## 4. DISCUSSION

This study presents the first analysis, to our knowledge, of seasonal ecological niches in a phylogenetic context, and supports the hypothesis that breeding season ecological niches are derived relative to winter ecological niches. Building on pioneer analyses (Joseph 1996, 2003; Joseph & Stockwell 2000) and a preliminary analysis of other taxa (Nakazawa *et al.* 2004), we analysed phylogenetic components of seasonal niches and distributions of the *Passerina* buntings in an explicitly phylogenetic context. Two of the species can clearly be designated 'niche followers' (*P. versicolor* and *P. amoena*), but three (*P. cyanea*, *P. ciris* and *P. caerulea*) show an odd asymmetry in which winter niches are highly predictive of breeding distributions, but not vice versa. The explanation of this pattern lies in the observation of qualitatively greater evolutionary change in breeding niches than in winter niches.

Our conclusion that ecological niches are highly conserved among wintering populations, but not among breeding populations, provides a first indication of the directionality of evolution of seasonal niches of migratory bird species. This result coincides well with the predictions of theory, in which tropically distributed species

'explore' extra-tropical distributional areas and eventually become established as breeders (Rappole 1995). This process is evidenced by recent northward range expansions by tropical taxa (e.g. *Euptilotis neoxenus* (Zimmerman 1978), *Tyrannus melancholicus* and *Heliomaster constantii* (AOU 1998)). The diversity of breeding niche characteristics raises the question of the directionality of evolution of migratory behaviour in this clade: although, at first glance, migratory behaviour in *Passerina* might best be explained as a single evolutionary derivation with some reversions to sedentary behaviour, an alternative highlighted by the dramatically divergent breeding niches is that these niches reflect several independent non-homologous derivations of migratory behaviour. More generally, this analysis represents a step towards the new phylogenetic perspective on the evolution of migratory systems called for by Zink (2002), and serves to illustrate the enormous complexity of evolutionary processes and ecological differentiation that makes up migratory systems.

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