

Ecomorphological pattern in Bermuda birds: the influence of competition and implications for nature preserves

JULIE L. LOCKWOOD¹ and MICHAEL P. MOULTON²

¹*Department of Zoology, University of Tennessee, Knoxville, TN 37996-0810, USA*

²*Department of Biology, LB 8042, Georgia Southern University, Statesboro, GA 30460-8042, USA*

Summary

Previous ecomorphological studies of introduced land birds on oceanic islands have revealed several patterns consistent with the hypothesis that interspecific competition influenced the assembly process of that community. We extend one of these analyses to Bermuda, which differs from the previous islands in its size, latitude and isolation from the mainland. We tested for the presence of morphological overdispersion in surviving introduced passeriforms. Despite a possible predominance of random events in the assembly process due to Bermuda's small size and the presence of migrant species, the surviving passeriforms were morphologically overdispersed. The presence of this pattern supports the hypothesis that the assembly of the Bermuda passeriform community has been influenced by interspecific competition. This marks the third distinct community of island land birds in which this competitive pattern has been identified. This is particularly interesting because certain attributes of Bermuda and its avifauna make it more equivalent to communities in mainland refuges than avian assemblages on islands studied previously. This suggests that interspecific competition may have important effects on the structure of refuge communities.

Keywords: Bermuda; community structure; competition; nature preserves; ecomorphology; passeriforms

Introduction

To say that a community is structured implies that the co-existing species in that community is a non-random sample drawn from a pool of potential colonizing species. Analyses of deliberately introduced species allow a more precise knowledge of which species in the pool colonized successfully and which species failed. Such analyses of the introduced avifaunas of the Hawaiian islands and Tahiti have demonstrated several community-wide patterns that appear to reflect the effects of interspecific competition on colonization (Moulton and Pimm, 1983, 1986, 1987; Moulton, 1985; Moulton and Lockwood, 1992; Lockwood *et al.*, 1993). Some of these results have sparked debate (Simberloff and Boecklen, 1991; Moulton, 1992). One persistent question involves determining the prevalence of such competitively mediated patterns in other avian communities. Recently, Lockwood *et al.* (1993) showed that surviving introduced passeriforms on Tahiti also show a competitive pattern: morphological overdispersion (see below). Here we extend these analyses to Bermuda which also has a rich history of documented species introductions dating back to the early 1800s. Bermuda, however, differs from Tahiti and Hawaii in size, latitude and isolation from the mainland.

One of the competitive patterns presented by Moulton and Pimm (1986, 1987) is directly testable with the avifauna of Bermuda, the pattern of morphological overdispersion, in which the

surviving species in a community are morphologically more different from one another than chance alone would predict (e.g. Moulton and Pimm, 1987).

Unlike other islands analysed, Bermuda harbours significant (although reduced) populations of native resident species in the same habitats into which the introduced species were released (Wingate, 1973; Crowell and Crowell, 1976). The main island is also much smaller than any previously studied, being only 51 km² (Bourne, 1957). Finally, Bermuda is host to many migrant species arriving throughout the year and having varying lengths of stay (Wingate, 1973).

In previous analyses, we assumed that any native species present on the islands were not interacting in any ecologically meaningful way with the 'pool' of introduced species (Moulton and Pimm, 1983, 1986, 1987; Moulton, 1992; Lockwood *et al.*, 1993). For example, in the Hawaiian islands there is a very clear separation between the community of introduced species and the native species. Any native species that are still present on the islands are restricted to higher elevations whereas the introduced species are found chiefly in the lowland habitats (see Scott *et al.*, 1986). On Tahiti there are only three native species, all of which are extremely rare (see Pratt *et al.*, 1987). Native-exotic interactions are probably negligible in their impact on the structure of the introduced avifauna (Moulton, 1993).

Conversely, Bermuda harbours three passerine species that have been common on the island since the first account of the fauna and flora was written in the 1880s (Bourne, 1957; Crowell, 1962). These are the Eastern Bluebird (*Sialia sialis*), the Bermuda White-eyed Vireo (*Vireo griseus*) and the Gray Catbird (*Dumatella carolinensis*) (Bourne, 1957). The White-eyed Vireo has been present long enough to be considered an endemic subspecies. The island is small in size and has relatively low habitat heterogeneity. The two communities (native residents and introduced species) may have interacted competitively.

The islands considered in previous analyses were relatively large (Tahiti, 1057 km² and Oahu, 1536 km²). On the one hand, the small size of Bermuda might obscure any community-wide competitive patterns by increasing the importance of random events (see Moulton and Pimm, 1986). Given that a small area will generally support populations at lower densities, it is possible that the vulnerability of these populations to extinction from random demographic events is increased (Terborgh and Winter, 1980; Shaffer, 1981; Pimm *et al.*, 1988). Further, weather events, of even marginal intensity, could have detrimental effects on populations at low densities.

On the other hand, a great deal of recent research on nested faunas (e.g. Patterson and Atmar, 1986) and on the effects of habitat fragmentation (Bolger *et al.*, 1991) suggests that the processes of colonization and extinction on small islands may be more deterministic than previously thought. In summary, it is possible, but not inevitable, that the small size of the island will inflate the importance of stochastic events to the point where they obscure the effects of deterministic processes, such as interspecific competition, in structuring communities.

There is a final unique attribute, the presence of migrant species on Bermuda, that poses an interesting problem. These species potentially compete with the resident species for food resources. The composition of the set of species which migrate to or through Bermuda each year, however, is highly influenced by weather events (Bourne, 1957). Wingate (1959) estimated that 120 passerine species have reached Bermuda and of these 75 occur regularly. Others have placed the total number of migrating species ever found on Bermuda at approximately 250 (Bourne, 1957) with 100 occurring regularly. We might suppose that fluctuating numbers and species composition of migrants might dilute any competitive interactions between the resident species (both native and introduced). Therefore, the chances of finding a community-wide competitive pattern might again be decreased by the possible predominance of unpredictable variation.

Materials and methods

The species

We compiled a list of the introduced species and their dates of introduction and estimated dates of extinction, using published reports (Bourne, 1957; Wingate, 1973; Long, 1981; Lever, 1987). We determined which species are now surviving on the island using the data of Wingate (1973) and personal field observations made in 1991. At least 14 passerine species have been introduced to Bermuda and of these seven have survived. Besides the three native residents, the seven introduced passerines that still persist are the Common Crow (*Corvus brachyrhynchos*), Great Kiskadee (*Pitangus sulphuratus*), Starling (*Sturnus vulgaris*), House Sparrow (*Passer domesticus*), European Goldfinch (*Carduelis carduelis*), Northern Cardinal (*Cardinalis cardinalis*) and Orange-cheeked Waxbill (*Estrilda melpada*). The Orange-cheeked Waxbill survives as a very small population in the only remaining mangrove forest on the island. The future of this species on Bermuda is extremely uncertain, but it was still present at the time of writing (D. Wingate, personal communication).

Eight of the 14 passerine introductions occurred sometime in the 19th century with the majority occurring in the 1870s. The Northern Cardinal is not mentioned in early accounts and is generally believed to have been introduced in the early 19th century (Bourne, 1957; Crowell, 1962; Wingate, 1973; Crowell and Crowell, 1976). The remaining six species were introduced in the late 20th century between the years of 1950 and the early 1970s. The majority of the early introductions were deliberate, whereas most 20th century introductions were accidental (that is, cage escapees or stowaways), with two notable exceptions; the Great Kiskadee, which was purposely introduced in 1957 as a biological control agent for an introduced *Anolis* lizard (Crowell and Crowell, 1976) and the European Starling, which colonized Bermuda from North America where it had been introduced in the 19th century (Lever, 1987). Despite the fact that the remaining 20th century introductions may involve the descendants of cage escapees, all the species included here showed evidence of breeding in Bermuda (see Lever (1987) for details of all introductions).

Morphological analysis

We measured at least six and as many as 18 museum specimens of each species at either the US National Museum of Natural History, Washington, DC or the LA County Museum of Natural History, Los Angeles, California. The measurements taken were as follows: wing chord (from the wrist to the tip of the longest primary), beak length (from the anterior margin of the nares to the tip of the upper mandible) and beak depth and width (at the anterior nares). In an attempt to correct for any sexual dimorphism in morphology, we tried to measure equal numbers of males and females. Occasionally, equal numbers of each sex were not available and, in some cases, the sex was not identified on the specimen tag.

Unfortunately specimens from Bermuda were not available. Crowell (1962) conducted a morphological comparison of the resident species of Bermuda to their North American counterparts and found no significant differences. This comparison included both the native residents and any introduced species that were present on the island at the time of writing. In light of this, we do not believe that an analysis based on measurements of Bermuda specimens would significantly alter the results of our analysis.

The characteristics we measured have been used in other analyses of this nature (e.g. Ricklefs and Cox, 1977; Moulton and Pimm, 1983, 1986, 1987; Miles and Ricklefs, 1984; Moulton and Lockwood, 1992; Lockwood *et al.*, 1993). Each characteristic chosen was assumed to be correlated with some aspect of avian ecology. Thus, wing length is believed to be the best

estimate of overall body size, although this might only hold for comparisons between species but not within species (see Rising and Sommers, 1989; Freeman and Jackson, 1990). The beak dimensions are assumed to be related to the type and size of food items taken (see Ashmole, 1968; Wilson, 1975; Ricklefs and Travis, 1980; Grant, 1986; Benkman and Pulliam, 1988).

We transformed the raw variables by calculating their common logarithms and then conducted a principal component analysis (PCA) by factoring the covariance matrix of these variables (Ricklefs and Travis, 1980). We calculated principal component scores for each individual of each species. We then calculated the mean principal component scores for each species. We plotted the 17 species introduced or native to Bermuda in the morphological space defined by the first two principal components.

Results

As is typical in principal component analyses of bird morphologies, the first two scores (PC I and II) accounted for more than 94% of the variance seen in the raw data. PC I had positive correlations with all the log transformed variables whereas PC II had positive correlations for the log of beak depth and width (Ln_d and Ln_w) and negative correlations with the log of the culmen and wing lengths (see Table 1). Since PC I had positive loadings for all the raw variables, it is interpreted as a measure of overall body size (Ricklefs and Travis, 1980). The second principal component (PC II) is interpreted as a measure of beak shape (i.e. beak thickness relative to body size). Principal components III and IV together accounted for less than 6% of the variance and we therefore discounted them in any further evaluation. The species used in the analyses and their principal component scores are listed in the Appendix.

We generated a plot using the principal component scores for each species (Fig. 1). In interpreting Fig. 1, those species which are plotted near the top right (positive scores) are the larger bodied, relatively thick-beaked species. Conversely, those species plotted near the bottom left (negative scores) are smaller bodied with relatively thin beaks.

To measure the morphological dispersion of the species, we used the minimal spanning tree (MST). The MST is the smallest sum of $n - 1$ line segments that connects n points such that no loops are created (Ricklefs and Travis, 1980). Each point corresponds to one of the species in the morphological space. Essentially, the MST is an estimate of the sum of interspecies morphological differences.

If a community is structured by interspecific competition then the observed MST value should exceed a large proportion (i.e. 95%) of the MST values for simulated communities containing the same number of species drawn at random from the pool of all species introduced to the community. Moreover, when plotted in a morphologically defined space the surviving species should be more evenly spaced than expected by chance. The degree of evenness in spacing can be

Table 1. Eigenvalues and Pearson product moment correlation coefficients between the first two principal components (PC I and PC II) and the log transformed variables for the 17 passeriform species introduced and native to Bermuda

	L_{wing}	L_{culmen}	Ln_d	Ln_w	Eigenvalue
PC I	0.79060	0.96640	0.85929	0.93421	0.068677
PC II	-0.56873	-0.21580	0.47498	0.28103	0.011714

L_{wing} through to Ln_w represent the log transformed raw variables.

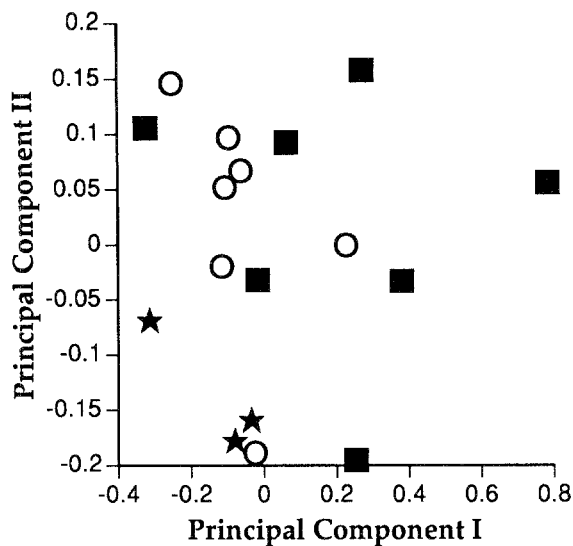


Figure 1. A plot of the 17 passeriforms of Bermuda according to their first two principal component scores. Solid squares indicate surviving introduced species, open squares indicate failed introduced species and solid stars indicate the three native species. See the Appendix for a list of principal component scores.

measured using the standard deviation (SD) for the $n - 1$ interspecies segments plotted in morphological space (Moulton and Pimm, 1987). The standard deviation observed for any set of $n - 1$ interspecies segments though, is positively correlated with the length of those segments. In other words, as the dispersion of the n points increases so will the standard deviation of the segments connecting those points. We determined unusually even spacing (i.e. relatively minimal variation in length between segments of the MST) by observing how many of the random MST lengths were simultaneously as large or larger than the observed MST and how many of those also had smaller standard deviations.

We computed MSTs and standard deviations for a series of randomly constructed communities and for the surviving set of 10 introduced and native species on Bermuda. Briefly, if N species survived and M species failed, we constructed null communities by randomly selecting N species from the total of $M + N$ species.

By acknowledging native–exotic interactions and thereby including natives in the analyses, we are sacrificing a degree of certainty about the composition of the species ‘pool’ (see Colwell and Winkler, 1984; Moulton and Lockwood, 1992). We have no way of knowing if other species attempted colonization along with the three natives and subsequently failed. In addition, although unlikely, it is nevertheless plausible, that the three native species maintain their Bermuda populations only through repeated colonizations from the North American mainland. If this were the case, the three natives must be considered permanent members of the Bermuda avifauna, since any local extinctions might not be recognizable.

For these reasons, we conducted our computer simulations in two ways. First, we combined the native and the introduced species into one group. Second, we forced the simulations to include the three natives in every random MST, thus considering the introduced species separately. For both methods, we calculated an MST for each of 1000 randomly assembled communities. Each randomly assembled community MST and associated standard deviation was then compared to that of the observed community (see Moulton and Pimm, 1986, 1987).

In the first simulation (when we gave each native and introduced species an equal chance of being drawn from the species pool), of 1000 randomly assembled communities, 58 had MST values as large or larger than the observed MST ($p = 0.058$). Moreover, only 14 of the 1000 communities were more evenly spaced and simultaneously as large or larger than the observed community ($p = 0.014$). In the second simulation we forced each randomly assembled community to include the three native species. The results obtained here did not differ qualitatively from those seen in the first simulation. Of 1000 randomly assembled communities 62 had MST values as large or larger than the observed ($p = 0.062$). However, only six of the 1000 random communities had an MST value as large or larger than the observed and simultaneously a smaller standard deviation of MST lengths ($p = 0.006$).

These results indicate that regardless of how we treat the surviving passeriforms of Bermuda (i.e. as a single group comprising both natives and exotics or when the exotics are treated separately from the natives) they are morphologically overdispersed. This pattern of morphological overdispersion is consistent with the hypothesis that interspecific competition has influenced the assembly of this community.

Discussion

The avifauna of Bermuda is morphologically overdispersed. This result extends to three, the number of distinct island communities in which we have observed patterns we attribute to interspecific competition (see Moulton (1992) and Lockwood *et al.* (1993) for the other two). This result is particularly interesting considering several of the characteristics of the island of Bermuda and its avifauna.

This marks the first attempt to find community-wide patterns in an island avifauna which has frequent and potentially strong interactions between native and introduced species. In addition, this is the smallest island and the only island which plays host to migrating species which were included in the morphological analyses. As we have pointed out, these two attributes could increase the chance that stochastic events rather than deterministic interactions, will predominate in shaping the community (Schoener and Schoener, 1983; Pimm *et al.*, 1988). Even under these circumstances, however, we have observed a pattern consistent with the hypothesis that interspecific competition shaped the composition of this community.

In answering the question of how prevalent the pattern of morphological overdispersion is, we can address another of equal importance: 'How durable are such patterns when we include conditions that more nearly approximate conditions seen in nature preserves?'. It has become a common practice to associate islands with refuges (see Simberloff and Abele, 1982; Wright and Hubbell, 1983). However, if we view past analyses of islands in this manner, inconsistencies emerge.

First, islands involved in previous analyses (Oahu and Tahiti) were typically larger and more isolated from sources of immigration. Second, communities of introduced bird species on Tahiti and Oahu probably do not significantly interact with the native species (Lockwood *et al.*, 1993; Moulton, 1993). The reduced level of isolation seen in Bermuda greatly increases the potential for negative interactions with seasonal migrant species. Janzen (1983) has pointed out that nature preserves may suffer similarly from interactions with invaders. Thus, the avifauna of Bermuda may more accurately reflect the circumstances of mainland nature refuges than other insular faunas that have thus far been studied. Finding community patterns consistent with the competition hypothesis under these circumstances suggests that in preserve situations the importance of interspecific competition cannot be ignored.

Acknowledgements

We thank Kimball Garrett and Richard Banks of the LA County Museum of Natural History and the US National Museum of Natural History, respectively, for allowing one of the authors (J.L.L.) access to their collections. For comments and editorial advice on various versions of this manuscript we thank Stuart L. Pimm. A special thanks to David Wingate for his help and advice concerning the visit to Bermuda of one of the authors (J.L.L.) and for sharing his extensive knowledge of the birds there. Partial funding from Georgia Southern University was provided to J.L.L. Computer time was provided by Georgia Southern University and the University of Tennessee, Knoxville.

References

- Ashmole, N.P. (1986) Body size, prey size, and ecological segregation in five sympatric terns (Aves: Laridae). *System. Zool.* **17**, 292–304.
- Benkman, C.W. and Pulliam, R.H. (1988) The comparative feeding rates of North American Sparrows and Finches. *Ecology* **69**, 1195–9.
- Bolger, D.T., Alberts, A.C. and Soule, M.E. (1991) Occurrence patterns of bird species in habitat fragments: sampling, extinction, and nested species subsets. *Am. Nat.* **137**, 155–66.
- Bourne, W.P. (1957) The breeding birds of Bermuda. *Ibis* **99**, 94–105.
- Colwell, R.K. and Winkler, D.W. (1984) A null model for null models in biogeography. In *Ecological Communities: Conceptual Issues and the Evidence* (D.R. Strong, Jr, D. Simberloff, L.G. Abele and A.B. Thistle, eds). Princeton University Press, Princeton, NJ.
- Crowell, K.L. (1962) Reduced interspecific competition among the birds of Bermuda. *Ecology* **43**, 75–88.
- Crowell, K.L. and Crowell, M.R. (1976) Bermuda's abundant, beleaguered birds. *Nat. History* **85**, 48–56.
- Freeman, S. and Jackson, W. (1990) Univariate metrics are not adequate to measure avian body size. *Auk* **107**, 69–74.
- Grant, P.R. (1986) *Ecology and Evolution in Darwin's Finches*, pp. 77–96. Princeton University Press, Princeton, NJ.
- Janzen, D.H. (1983) No park is an island: increase in interference from outside as park size decreases. *Oikos* **41**, 402–10.
- Lever, C. (1987) *Naturalized Birds of the World*. Longman Scientific and Technical, New York.
- Lockwood, J.L., Moulton, M.P. and Anderson, S.K. (1993) Morphological assortment and the assembly of communities of introduced passeriforms on oceanic islands: Tahiti versus Oahu. *Am. Nat.* **141**, 398–408.
- Long, J. (1981) *Introduced Birds of the World*. David and Charles, London.
- Miles, D.B. and Ricklefs, R.E. (1984) The correlation between ecology and morphology in deciduous forest passerine birds. *Ecology* **65**, 1629–40.
- Moulton, M.P. (1985) Morphological similarity and co-existence of congeners: an experimental test with introduced birds. *Oikos* **44**, 301–5.
- Moulton, M.P. (1993) The all-or-none pattern in introduced Hawaiian passeriforms: the role of competition sustained. *Am. Nat.* **141**, 105–19.
- Moulton, M.P. and Lockwood, J.L. (1992) Morphological dispersion of introduced Hawaiian finches: evidence for competition and a Narcissus effect. *Evol. Ecol.* **6**, 45–55.
- Moulton, M.P. and Pimm, S.L. (1983) The introduced Hawaiian avifauna: biogeographical evidence for competition. *Am. Nat.* **121**, 669–90.
- Moulton, M.P. and Pimm, S.L. (1986) The extent of competition in shaping an introduced avifauna. In *Community Ecology* (J. Diamond and T. Case, eds). Harper & Row, New York.
- Moulton, M.P. and Pimm, S.L. (1987) Morphological assortment in introduced Hawaiian passerines. *Evol. Ecol.* **1**, 113–24.
- Patterson, B.D. and Atmar, W. (1986) Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biol. J. Linn. Soc.* **28**, 65–82.

- Pimm, S.L., Jones, H.L. and Diamond, J. (1988) On the risk of extinction. *Am. Nat.* **132**, 756–77.
- Pratt, D.H., Bruner, P.L. and Berrett, D.G. (1987) *The Birds of Hawaii and Their Tropical Pacific*. Princeton University Press, Princeton, NJ.
- Ricklefs, R.E. and Cox, G.W. (1977) Morphological similarity and ecological overlap among passerine birds on St. Kitt, British West Indies. *Oikos* **29**, 60–6.
- Ricklefs, R.E. and Travis, J. (1980) Morphological approach to the study of avian community organization. *Auk* **97**, 321–38.
- Rising, J.D. and Somers, K.M. (1989) The measurement of overall body size in birds. *Auk* **106**, 666–74.
- Schoener, T.W. and Schoener, A. (1983) Distribution of vertebrates on some very small islands. II. Patterns in species number. *J. Anim. Ecol.* **52**, 237–63.
- Scott, J.M., Mountainspring, S., Ramsey, F.L. and Kepler, C.B. (1986) *Forest Bird Communities on the Hawaiian Islands: Their Dynamics, Ecology, and Conservation*. Cooper Ornithological Society, Berkeley, CA.
- Shaffer, M.L. (1981) Minimum population sizes for species conservation. *Bioscience* **31**, 131–4.
- Sibley, C.G. and Monroe, B.L. Jr. (1990) *Distribution and Taxonomy of Birds of the World*, Yale University Press, New Haven and London, UK.
- Simberloff, D.S. and Abele, L.G. (1982) Refuge design and island biogeographic theory: effects of fragmentation. *Am. Nat.* **120**, 41–50.
- Simberloff, D.S. and Boecklen, W. (1991) Patterns of extinction in the introduced Hawaiian avifauna: a re-examination of the role of competition. *Am. Nat.* **138**, 300–27.
- Terborgh, J. and Winter, B. (1980) Some causes of extinction. In *Conservation Biology* (M. Soule and B.A. Wilcox, eds), pp. 119–34. Sinauer Associates, Sunderland, MA.
- Wilson, D.S. (1975) The adequacy of body size as a niche difference. *Am. Nat.* **109**, 769–84.
- Wingate, D. (1959) *A Checklist of the Birds, Mammals, Reptiles, and Amphibians of Bermuda*. Bermuda Audubon Society, Hamilton, Bermuda.
- Wingate, D. (1973) *A Checklist and Guide to the Birds of Bermuda*. Island Press, Hamilton, Bermuda.
- Wright, S.J. and Hubbell, S.P. (1983) Stochastic extinction and reserve size: a focal species approach. *Oikos* **41**, 466–76.

Appendix

Mean principal component scores (PC I and PC II) and dates of introduction for each of the 17 introduced and native species of Bermuda

Species	Date introduced	PC I	PC II
<i>Cardinalis cardinalis</i> (S)	1800	0.27401	0.15074
<i>Carduelis carduelis</i> (S)	1800	−0.01512	−0.03374
<i>Carduelis tristis</i>	1800	−0.11366	−0.01999
<i>Corvus brachyrhynchos</i> (S)	1876	0.78381	0.05493
<i>Dumetella carolinensis</i> (S)	Nat	−0.03462	−0.15873
<i>Estrilda astrild</i>	1970	−0.24975	0.14568
<i>Estrilda melpoda</i> (S)	1970	−0.32182	0.10525
<i>Euplectes orix</i>	1970	−0.09389	0.09677
<i>Mimus polyglottos</i>	1893	−0.02320	0.18886
<i>Passer domesticus</i> (S)	1870	0.06369	0.09205
<i>Passer montanus</i>	1800	−0.06152	0.06697
<i>Pitangus sulphuratus</i> (S)	1957	0.38233	−0.03393
<i>Ploceus capensis</i>	1970	0.22828	−0.00066
<i>Serinus canaria</i>	1968	0.10510	0.05183
<i>Sialia sialis</i> (S)	Nat	−0.07480	−0.17754
<i>Sturnus vulgaris</i> (S)	1950	0.25321	−0.19566
<i>Vireo griseus</i> (S)	Nat	−0.31310	−0.06276

Successful species are designated by (S). Nomenclature follows Sibley and Monroe (1990).