

# Change in wing morphology of the European starling during and after colonization of North America

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## Keywords

invasive species; migration; range expansion; hand-wing index; dispersal; macro-evolution; urbanization; geographic variation.

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Editor: Andrew Kitchener

Received 22 August 2014; revised 13 November 2014; accepted 18 November 2014

doi:10.1111/jzo.12200

## Abstract

When exposed to a new area and the potential for range expansion, species may quickly evolve morphological traits that allow them to colonize novel habitat. How quickly these changes occur and how long they subsequently persist in the established population has rarely been documented in birds. The European starling has been introduced in a number of areas around the world, including North America where an initially small population was established in 1890 and 1891. Their prolific expansion westward across the continent occurred at a tremendous rate of up to 90 km/year. We hypothesized that the individuals leading the expansion wave had longer and pointier wings because these characteristics are associated with greater juvenile dispersal distances. Therefore, we predicted that successive generations of range expanding birds would display increasing wing length and pointedness. Using museum specimens collected in North America since their introduction, we tested this hypothesis and examined temporal patterns to determine if wing shape changed following the establishment of local populations after the initial colonizing phase. Contrary to our expectations, wing length and shape did not change during the colonization wave. However, the pointedness of European starling wings decreased across the continent by more than 3.8% over the last 120 years. This was caused by an increase in the length of the secondary feathers, not by a decrease in the length of primary feathers. We discuss these results in the context of increased afforestation and urbanization during that time, and the potential benefit of rounder wings for foraging and predator avoidance.

## Introduction

Species introduced to novel areas may find themselves relieved of previous environmental pressures, but may also be confronted with the requirements of new habitats (Zenni *et al.*, 2014). How species respond to an introduction can inform us about the adaptive function of phenotypic variation (Moloney *et al.*, 2009), and the rate at which macro-evolutionary changes occur (Lee, 2002; Lindström *et al.*, 2013). Given that the introduction and subsequent establishment of invasive non-indigenous species may pose negative effects for native species and their ecosystems (Mooney & Cleland, 2001), determining what traits make species successful at colonizing new areas is important for understanding how to manage and prevent future invasions (Carlton & Ruiz, 2003).

Several factors, both anthropogenic and intrinsic to specific species, explain why some invasive species successfully establish populations following their introduction. Of these, introduction effort, fecundity and phenotypic plasticity are some of the most influential (O'Connor *et al.*, 1986; Duncan *et al.*, 2001; Sakai *et al.*, 2001; Sol, Timmermans & Lefebvre, 2002; Duncan, Blackburn & Sol, 2003). In some instances, newly established populations evolve quickly, with physiological,

behavioural and morphological traits diverging among populations (Williams & Moore, 1989; Hill, Thomas & Blakeley, 1999; Lee, 2002). In two species of crickets *Conocephalus discolor* and *Metrioptera roeselii*, for example, Simmons & Thomas (2004) showed that populations located near the edge of their expanding range had longer wings and greater rates of dispersal, which facilitated rapid population expansion. Not surprisingly, a species' ability to disperse profoundly affects its ability to colonize new territory (Weeks & Claramunt, 2014). In birds, the shape and length of wings determines how an individual can manoeuvre, how fast it can travel (Tittler, Villard & Fahrig, 2009) and its propensity to disperse (Dawideit *et al.*, 2009). Pointed wings, with greater aspect ratio and relatively longer lift-inducing leading edges, are found in long-distance migrants and in species with longer juvenile dispersal distances (Monkkonen, 1995; Lockwood, Swaddle & Rayner, 1998). In contrast, rounded wings offer increased manoeuvrability, but are associated with shorter juvenile dispersal distances (Dawideit *et al.*, 2009). Pointier and longer wings would allow for rapid colonization of a large territory, and the population at the front of the expansion wave would be composed of individuals with greater juvenile dispersal rates and associated longer and/or pointier wings

(i.e. spatial sorting; Phillips, Brown & Shine, 2010; Shine, Brown & Phillips, 2011). Because wing morphology is heritable in birds (e.g. Merilä & Sheldon, 2000; Jensen *et al.*, 2003), succeeding generations of colonizers would display increasing wing length and wing pointedness. As a result, the size and shape of wings would be expected to change during the colonization of a novel area, yet such changes have rarely been investigated (see Skjelseth *et al.*, 2007 for an exception).

In this study, we investigate wing shape and size in the European starling *Sturnus vulgaris* following their introduction to North America. This species was first introduced to North America in 1890 and 1891, when *c.* 80 breeding pairs from England were released in Central Park, New York (Phillips, 1928). The European starling is now perhaps the most abundant bird species in North America. Expanding its range rapidly, it reached the west coast of North America by the early 1950s, and is now widely distributed throughout the continent (Cabe, 1993). Population expansion models, combined with observational data, estimate that this species expanded its range at a rate of 77–91 km/year (van den Bosch, Hengeveld & Metz, 1992). As a species that prefers edge habitat, the expansion of starlings has been aided by human disturbance and, in particular, by the conversion of natural habitat to agriculture areas. The success of the European starling has been attributed to its ability to adapt to fluctuating thermal environments (Johnson & Cowan, 1974). However, the question remains as to whether morphological changes occurred during the colonization process which may have aided starlings during their westward expansion.

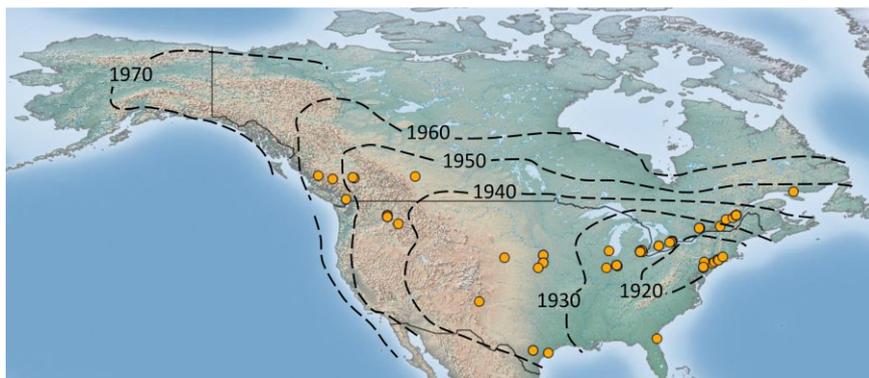
We surveyed museum specimens of European starlings collected since their introduction to investigate changes in wing morphology following their colonization of North America. First, because starlings with the longest dispersal distance and associated longer and pointier wings would lead the colonization front, we predicted that successive generations of range expanding birds would display increasing wing length and pointedness. Second, we examined temporal patterns of wing morphology to determine if wing shape changed following the establishment of local populations. We predicted that wing length would shorten and wing shape would become more rounded following colonization, given that individuals would

benefit from increased manoeuvrability for foraging and predator avoidance.

## Materials and methods

We targeted museum skins of North American specimens collected during the starling's range expansion. Our initial search identified all adult starling specimens available from the US and Canada in all museums indexed in ORNIS (<http://www.ornisnet.org/>; retrieval date 17 January 2012). We initially selected specimens that were the first to be collected in a newly colonized area, and only kept those that were likely to have been collected within the first 5 years of a newly colonized area by using Johnson & Cowan's (1974; Fig. 1) colonization isopleths map and Kessel's (1953) detailed summary of starling range expansion. Including specimens captured more than 5 years after colonization potentially decreases the chances of detecting changes in wing morphology because traits that evolve at the leading edge of a colonization wave can revert back to original values within 5–10 years (Simmons & Thomas, 2004; Brown, Phillips & Shine, 2014). All specimens were geo-referenced using the data available on ORNIS or the locality indicated on the information tag. To evaluate how wing shape and size changed after colonization, we then selected skins from nearby locations (within 100 km) collected in subsequent years up to 2010. If more than four skins were available from the same location for the same year post colonization, we limited our sampling to a randomly selected subset of four skins.

We noted from the information tag the year birds were collected, their sex and any mentions pertinent to the colonization event. We categorized birds as being part of the colonizing wave if collected within the first 5 years of the range expansion using the criteria described above; to be more conservative in some of our analyses, we categorized only the subset of birds collected within the first 3 years of the range expansion as colonizers. Birds collected later were categorized as non-colonizing birds. Starlings moult only once a year; their spotted winter plumage changes to an iridescent summer plumage with wear of the feather tips (Cabe, 1993). To include the potential effect of feather wear in our analyses, we



**Figure 1** Isopleths indicate the estimated range expansion of the European starling *Sturnus vulgaris* following their introduction in New York's Central Park in 1890 and 1891 (following Johnson & Cowan, 1974). Symbols denote provenance locations of museum specimens that were captured during the range expansion and used in this study.

classified the birds as bearing summer or winter plumage based on the amount of white on the secondary covert tips.

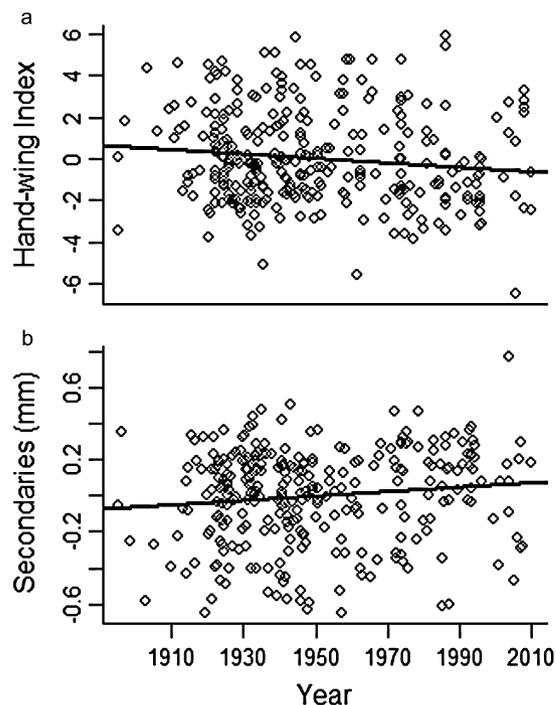
For each skin, we measured to the nearest 0.1 mm using callipers: culmen length from the proximal end of the nares to the tip of culmen (as a 'control' measure following Desrochers, 2010), wing chord, and carpal joint to end of the outermost secondary feather. The same person (P-P. B.) repeated the measurements three times, and statistical tests used averages. We measured a subset of 25 skins twice (non-sequentially) to evaluate measurement repeatability (Lessells & Boag, 1987). As a measure of wing shape, we calculated the hand-wing index (following Desrochers, 2010; Weeks & Claramunt, 2014) as  $\text{hand-wing index} = (\text{wing chord} - \text{distance from the carpal joint to the tip of the longest secondary feather}) / \text{wing chord}$  (Leisler & Winkler, 1991; Dawe *et al.*, 2009). Rounded wings have relatively smaller hand-wing values and pointed wings have relatively greater hand-wing index.

To understand the changes in wing length and shape during and after the colonization of North America by starlings, we conducted five multifactor linear regression analyses with stepwise removal of non-significant factors. To investigate changes immediately after the introduction, the first analysis included the hand-wing index of only the colonizing birds as the dependent variable and year, sex, season (winter or summer), latitude and first-level interactions as the independent factors. Longitude was not included because it was highly correlated with year. The second analysis included the wing chord of colonizing birds only as the dependent variable and the same independent factors as the previous analysis. To investigate overall changes in wing morphology, the third analysis included the hand-wing index of all birds as the dependent variable and included year, sex, season, latitude, longitude and all first-level interactions. The fourth and fifth analyses included the length of the secondaries and the wing chord of all birds as the dependent variables and the same independent factors as the previous analysis. These two tests were conducted to determine if changes in wing shape occurred because of changes to the secondary flight feathers or to the overall wing length. Finally, we analysed whether culmen length had changed since colonization to determine if temporal changes in wing morphology were mirrored by another morphological trait using year, sex, latitude, longitude and first-level interactions as dependent variables. We consider statistical significance at  $\alpha = 0.05$  and present mean  $\pm$  standard error.

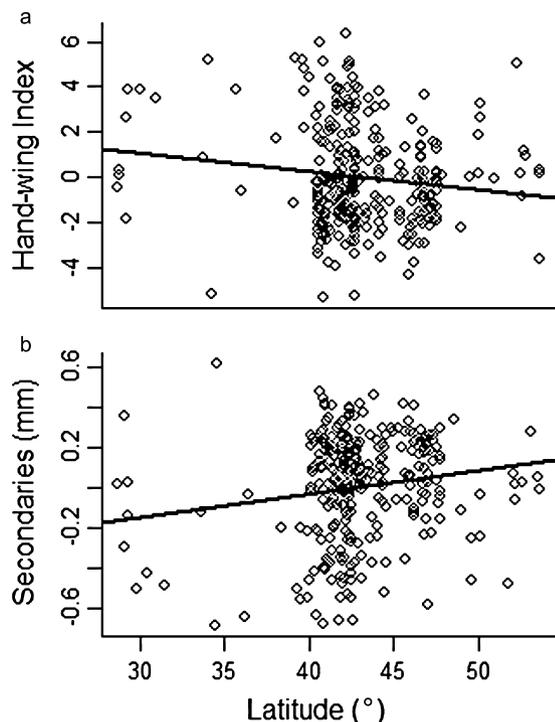
## Results

We obtained morphological measurements on 312 bird skins of which 82 were collected within 5 years of the starling's range expansion (Fig. 1). In five different instances, notes on the tag indicated that the collected birds were the first ever seen in the area, and corresponded with isopleth estimations identified by Johnson & Cowan (1974). Repeatability of all three measurements was very high ( $R^2 > 0.95$  for all three morphological traits).

In the linear regression analysis that included only the 82 colonizing birds, we did not find any factors that predicted the hand-wing index, but the analysis for wing chord indicated that males had longer wings ( $12.64 \pm 0.04$ ) than females ( $12.44 \pm 0.06$ ;  $t = 2.82$ ,  $P = 0.006$ ). Including only birds captured during the first 3 years of the range expansion produced similar results; none of the factors predicted the hand-wing index score and males had longer wings ( $12.65 \pm 0.04$ ) than females ( $12.44 \pm 0.06$ ;  $n = 70$ ,  $t = 2.98$ ,  $P = 0.004$ ). The linear regression analysis with hand-wing index as the dependent variable which included all 312 birds generated a statistically significant model ( $F_{2,307} = 5.68$ , adjusted  $R^2 = 0.03$ ,  $P = 0.004$ ) with two parameters. This model suggested that the hand-wing index decreased over the course of the last 120 years at a rate of 3.8% per 100 years (slope:  $-0.0107 \pm 0.005$ ,  $t = -2.20$ ,  $P = 0.028$ ; Fig. 2a) and decreased with greater latitude (slope:  $-0.0813 \pm 0.034$ ,  $t = -2.38$ ,  $P = 0.018$ ; Fig. 3a). The model that best fit the secondary feather length data included four parameters ( $F_{4,289} = 16.97$ , adjusted  $R^2 = 0.18$ ,  $P < 0.001$ ). It suggested that the secondary flight feathers increased with wing length (slope:  $0.3105 \pm 0.053$ ,  $t = 5.81$ ,  $P < 0.001$ ), increased in length over the last 120 years (slope:  $0.0012 \pm 0.0005$ ,  $t = 2.09$ ,  $P = 0.038$ ; Fig. 2b), were longer in males than in females (parameter estimate:  $0.0906 \pm 0.033$ ,  $t = 2.74$ ,  $P = 0.006$ ) and increased with latitude (slope:  $0.0115 \pm 0.004$ ,  $t = 2.79$ ,



**Figure 2** The hand-wing index (unitless) of the wing of European starling *Sturnus vulgaris* has (a) decreased by more than 3.8% over the last 120 years due to (b) an increase in the length of the secondary feathers during that time. Diagrams are partial regression plots and present the relationships after controlling for other significant factors in linear regression models (see Results section).



**Figure 3** The hand-wing index (unitless) of the European starling *Sturnus vulgaris* (a) decreases with increasing latitude across North America. This is not due to a change in the length of the wing chord but to (b) an increase in the length of the secondary feathers with increase in latitude. Diagrams are partial regression plots and present the relationships after controlling for other significant factors in linear regression models (see Results section).

$P = 0.006$ ; Fig. 3b). In contrast, the model that best fit the wing chord data indicated that males had longer wings (parameter estimate:  $0.1900 \pm 0.034$ ,  $t = 5.57$ ,  $P < 0.001$ ) but there was no effect of year as in the previous models. Culmen length was larger in males ( $2.17 \pm 0.012$  mm) than in females ( $2.10 \pm 0.013$  mm;  $n = 285$ ,  $t = 5.571$ ,  $P < 0.001$ ) but was not predicted by any other factors.

## Discussion

In this study, we set out to evaluate changes in wing morphology in the population of European starlings that colonized North America. Contrary to our expectations, we did not find any evidence of an increase in the hand-wing index or in wing length of starlings colonizing westward, despite these attributes being generally considered more beneficial for dispersal, and during range expansion (Skjelseth *et al.*, 2007; Dawideit *et al.*, 2009). However, our data suggest that the hand-wing index of European starlings has decreased by more than 3.8% over a relatively brief time span (~120 years), and that this was caused by an increase in the length of the secondary flight feathers, not a decrease in the overall wing chord.

Rapid changes in phenotype following introductions, or as a result of environmental changes, are known to have

occurred in a number of vertebrate and invertebrate species (e.g. Boag & Grant, 1981; Simmons & Thomas, 2004; Phillips *et al.*, 2006). In an experimental introduction of *Anolis* lizards, for example, populations translocated onto different islands, and with different vegetation, diverged from one another in ways that made them better adapted to their environments within 10–14 years (Losos, Warheit & Schoener, 1997). Similarly, wing shape and frequency of wing shape types changed in cricket populations at the forefront of a range expansion (Simmons & Thomas, 2004). These changes in wing shape were short term, however, and disappeared within 5–10 years following the initial expansion with long-winged individuals becoming far less common than during range expansion (Simmons & Thomas, 2004). Our study did not demonstrate any wing changes during expansion. Therefore, it could be argued that our study did not adequately sample the front range of the expansion, and did not capture the individuals that may have undergone rapid evolutionary changes. However, we do not believe this to be the case. First, we were able to obtain specimens captured as early as 1897, only 6–7 years post release, when the population had not started their rapid westward expansion. Second, information on the tags confirmed that some of the specimens collected were the first ever detected in an area, and agreed with the isopleth determined by Johnson & Cowan (1974) and the detailed accounts summarized by Kessel (1953). Third, a plot of distance travelled and collection year of the skins included in the ‘colonizer’ category showed a very tight exponential growth relationship (adjusted  $R^2 = 0.90$ ), suggesting that we did not include individuals far behind the colonizing front when categorizing a specimen as being part of the ‘colonizer’ group. Finally, using a stricter criterion for inclusion in the ‘colonizer’ group (3 years after the front of the wave rather than 5 years) did not qualitatively alter any of the findings. Therefore, we most likely failed to detect any changes in wing morphology in the colonizing population because no change occurred, not because of a methodological or design flaw.

Failure to detect changes in wing morphology could be due, in part, to adult dispersal and migration. While the population of European starlings introduced in Central Park by the American Acclimatization Society was likely from resident birds (Phillips, 1928; Feare & Craig, 1999), some of the current North American populations migrate (Cabe, 1993). Even non-migratory populations can travel large distances, mainly during winter foraging bouts (Hamilton *et al.*, 1967; Royall *et al.*, 1972; Cabe, 1999). Adult dispersal resulting from these movements would reduce the gradation of wing size and shape along the colonizing front by mixing long-distance juvenile dispersers with short-distance dispersers. It is also possible that the relationship between wing shape and juvenile dispersal is not as strong in European starlings as it is in other species, or that traits other than wing morphology promoted the fast dispersal across the continent. Studies on North American and South African starlings (Hui *et al.*, 2012) have demonstrated accelerating dispersal rates during the colonization of these non-native ranges, presumably as a consequence of spatial sorting. Other traits, such as the propensity to disperse in a straight line, which does not need to be correlated

with wing morphology, could be responsible for these patterns (Brown *et al.*, 2014).

We detected a decrease in hand-wing index of about 3.8% per 100 years. Even though some morphological traits of museum specimens can change over time (e.g. degradation of carotenoid pigments and subsequent fading of plumage coloration; Armenta, Dunn & Whittingham, 2008; Doucet & Hill, 2009), the structures we measured to quantify wing shape are only composed of bone and keratin, which are not expected to change over time. Indeed, wing chord measurements of live and museum specimens of the same species do not differ significantly (e.g. Sandoval & Mennill, 2013). Therefore, the increased roundness of the wing shape we detected over 120 years is not likely to be an artefact of specimen aging. Recent work by Desrochers (2010) has shown that the wing shape of many North American songbird species has changed over the last 100 years, likely in response to habitat changes. In his study, 12 of 21 species experienced a significant change in wing shape during that time span, five of which had changed by 3.8% or more. At least two non-mutually exclusive factors could have driven the evolution for rounder wings in starlings. First, as Desrochers (2010) argued, afforestation of open habitat which occurred in many parts of the US during the 20th century (Foster & Motzkin, 2003) would have driven the evolution of rounder wings in species traditionally occupying these environments. More common edge habitat increases the need for navigation through dense vegetation which should favour the evolution of rounded wings (Marchetti, Price & Richman, 1995; Forstmeier & Keßler, 2001). Second, starling populations have expanded in association with increased urbanization (Cabe, 1993). Urban areas contain higher concentrations of predators (Sorace, 2002), and the ability to avoid and escape predators could have influenced the trajectory of changes in wing shape. Indeed, starlings with rounder wings have better take-off ability (Swaddle & Lockwood, 2003) which increases predator escape efficiency (Forstmeier & Keßler, 2001; Swaddle & Lockwood, 2003). Therefore, both increased afforestation and urbanization may have influenced wing shape changes over the last ~100 years.

Our results suggest that the wings of starlings are increasingly rounder with increased latitude because of an increase in the length of the secondary flight feathers, not a decrease in the wing chord. It is common among North American bird species that northern populations migrate while southern populations are non-migratory (Elphick, 2011), and shorter and rounded wings are a characteristic of many resident bird populations in North America (Monkkonen, 1995; Rasner *et al.*, 2004). Some European starlings from populations in the Eastern and Midwestern US migrate (Dolbeer, 1982), but there is no migratory trend applicable to the geographic range of our samples. Furthermore, if migration behaviour influenced wing shape in starlings, we would expect a trend opposite to the one we detected. Across and within species, it is not unusual for individuals in more northern climate to be larger in size to reduce the volume to surface-area ratio (Bergmann's rule; Bergmann, 1847; Brommer *et al.*, 2014; Hassall *et al.*, 2014). However, culmen length and wing chord measurements

from our samples do not show any trend with changes in latitude, suggesting that this mechanism is unlikely. Alternatively, following Allen's rule (Allen, 1877; Nudds & Oswald, 2007) that suggests the body shape of individuals in cooler locations is functionally modified to reduce heat loss, it is possible that the secondary flight feathers provide more insulation to the back and rump of the birds, and thus provide better thermal cover. This hypothesis could not be properly tested with our data; measurements on the length and density of insulating feathers (down and semiplumes) would better address this question.

While we could not directly demonstrate an effect of colonization on the evolution of a morphological characteristic, our study demonstrates evolutionary changes in the wing shape of a widely distributed introduced species in North America. The hand-wing index in the starling has decreased by more than 3.8% in the last ~120 years. Rounded wings have likely contributed to the success of this species, given that rounded wings have been shown to improve foraging efficiency (Forstmeier & Keßler, 2001) and predator avoidance (Swaddle & Lockwood, 2003). Further work should incorporate morphological measurements from starlings with different levels of urbanization to determine the root cause of the changes we detected.

## Acknowledgements

We thank, first and foremost, Janet Hinshaw of the University of Michigan Museum of Zoology for all of her help, especially the handling of many loaned specimens. We thank Mark Peck of the Royal Ontario Museum for hosting us at their research collection. We are grateful to several curators and collection managers who agreed to loan us study skins: Michel Gosselin of the Canadian Museum of Nature, Kelly Cassidy of the Charles R. Conner Museum, Kristof Zyskowski of the Yale Peabody Museum, Thomas Labeledz of the University of Nebraska State Museum, David Willard of the Field Museum of Natural History, and Tom Trombone and Paul Sweet of the American Museum of Natural History. We thank Stéphanie M. Doucet as well as current and past members of the Doucet and Mennill Labs. L. Sandoval, R. Sosa, D.R. Wilson and two anonymous reviewers provided valuable comments that improved previous versions of the paper. This research was made possible by a Field Museum Visiting Scholar Grant, and a Natural Sciences and Engineering Research Council of Canada Graduate Scholarship to P-P. B. Data used in this study are available upon request.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

**Table S1.** Accession numbers of museum specimens measured for this study. AMNH: American Museum of Natural History, New York; CMN: Canadian Museum of Nature, Ottawa; CRCM: Charles R. Conner Museum, Washington; ROM: Royal Ontario Museum, Toronto; UMMZ: University of Michigan Museum of Zoology, Ann Arbor; UNSM: University of Nebraska State Museum, Lincoln; YPM: Yale University Peabody Museum, New Haven.