

Article

Museum-Based Research on the Lice (Insecta: Phthiraptera) Infestations of Hummingbirds (Aves: Trochilidae)—Prevalence, Genus Richness and Parasite Associations

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Abstract: We documented the presence/absence of the eggs of *Trochiloecetes*, *Trochiliphagus*, and *Leremenopon* lice on over 50,000 hummingbird specimens (representing 348 species plus 247 additional subspecies) in four museums in the USA. (i) We provide sample estimates of infestation prevalence. (ii) Sample estimates of parasite genus richness increased with increasing host sample size. (iii) Host body mass did not correlate with parasite genus richness, even when controlled for sample size effects. (iv) The prevalence of *Trochiliphagus* and *Trochiloecetes* infestations did not correlate with host body mass, while the prevalence of *Leremenopon* exhibited a marginally significant positive correlation with host body mass. (v) The prevalence of *Trochiliphagus* and *Leremenopon* infestations correlated strongly and positively across host taxa (i.e., species or subspecies). (vi) The co-occurrence of *Trochiliphagus* and *Trochiloecetes* within the few largest host samples—i.e., within particular host taxa—was significantly more frequent than expected by chance. This latter association might indicate a true ecological relationship or, alternatively, might have emerged as an artifact of our sampling method. (vii) We found no relationship between host sexual size dimorphism and the prevalence of any of the three louse genera, contrary to the interspecific prediction of the Hamilton–Zuk hypothesis.

Keywords: *Phthiraptera*; *Amblycera*; *Trochilidae*; ecology; neotropics; Hamilton–Zuk hypothesis; sampling bias



Citation: Oniki-Willis, Y.; Willis, E.O.; Lopes, L.E.; Rózsa, L. Museum-Based Research on the Lice (Insecta: Phthiraptera) Infestations of Hummingbirds (Aves: Trochilidae)—Prevalence, Genus Richness and Parasite Associations. *Diversity* **2023**, *15*, 54. <https://doi.org/10.3390/d15010054>

Academic Editors: Michael Wink, Luc Legal, Ben-Erik Van Wyk and Michel Baguette

Received: 5 December 2022

Revised: 23 December 2022

Accepted: 24 December 2022

Published: 3 January 2023



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1. Introduction

Parasitic lice (Insecta: *Phthiraptera*) are small-bodied, wingless insects that complete their whole life cycle as permanent ectoparasites of most—if not all—species of birds and several taxa of mammals [1]. They are primarily transmitted through direct body-to-body contact among hosts. Lice infestations typically exhibit a low level of virulence, not severely debilitating host birds [2]. However, they still influence significant aspects of hosts' life history, including sexual selection [3], metabolism [4] and perhaps even survival [5]. Since they are larger than any other contagious pathogens of birds and mammals, lice are relatively easy to study. They firmly attach their eggs, often called nits, to feather shafts or between feather barbs, and the empty egg capsules remain fixed there long after the larvae hatch, up to the next molt [1,6]. The suborder of Amblyceran lice have retained some of the more primitive features of this insect order. They feed on skin debris and often chew developing feathers and soft areas of the skin, causing localized bleeding from which

they drink fluids [7]. Concomitantly, they may provoke an immune response from the host when feeding on living tissues [8].

Hummingbirds (Aves: *Trochilidae*) are relatively small-bodied birds, with all the currently recognized 361 species [9] restricted to the Americas. They feed primarily on flower nectar, insects and spiders [10]. Their mating system is polygamous; males do not participate in nesting and brood care. Accordingly, several species exhibit sexual dimorphism in body size [11,12], colors [13] and sometimes even in bill structure [14].

Hummingbird-infesting lice were first reviewed by Carriker in 1960 [15]. Despite the large number of hummingbird species [9], only 50 species of lice representing four genera have been described to date, with all of them belonging to the suborder *Amblycera* [16–18]. Two genera, *Trochiloecetes* and *Trochiliphagus* (Ricinidae), are exclusive to hummingbirds. The latter genus, *Trochiliphagus*, was synonymized with *Ricinus* by Rheinwald [19], a taxonomical decision not widely accepted [20] and, therefore, not followed by the authors. Both genera exhibit an archaic morphology and are exceptionally large-bodied relative to their hosts' body size [21]. In addition, they possess piercing mouthparts and consume blood [22]. The two other genera infesting hummingbirds are *Leremenopon* and *Myrsidea* (Menoponidae) [17,18]. The former is exclusive to hummingbirds, while the latter is a cosmopolitan genus widespread mostly among passerines but, with few remarkable exceptions, is rare or sporadic as a parasite of hummingbirds. They are much smaller-bodied than the former two genera, possessing chewing mouthparts and consuming skin fragments and tissue fluids [7]. Unlike most other birds, hummingbirds and their sister clade, the swifts (Apodidae) [23], do not host Ischnoceran lice. Studies of Neotropical lice are at the alpha taxonomic level; their biology and ecology are poorly understood [20,24].

Our present study aims to provide descriptive statistics of hummingbirds' louse infestations and to search for potential ecological factors shaping the prevalence of these infestations. For this purpose, we sampled museum specimens of hummingbirds and identified louse eggs (including empty nits) fixed to their feathers. Eggs were identified to the genus level, and their presence or absence indicated the infestation status of birds. The theoretical background behind our study, the hypotheses investigated, and their respective predictions are presented below.

Early authors [25] proposed that large-bodied birds tend to be 'lousier' than small-bodied species. This observation was verified by phylogenetically controlled tests comparing the mean abundance of lice across host species [26]. However, anecdotal evidence suggests that this is not necessarily true for ricinid lice (such as *Trochiliphagus* and *Trochiloecetes* in our study) because this family appears to be specific to small-bodied hosts, namely hummingbirds and some small- to medium-sized passerines [21,27]. In this paper we take the opportunity to test if large-bodied hummingbird species are 'lousier' than small-bodied species.

Hamilton and Zuk [28] proposed a model of sexual selection that explains how females' preference for male secondary sexual characters that indicate resistance to parasites could maintain genetic variation in host species. This model has been theoretically examined and empirically tested across several taxa; however, it has turned out to be extremely difficult to demonstrate [29]. Nevertheless, one of its predictions, which postulates a positive covariation between host sexual dimorphism and the prevalence of parasitic infections, is easy to test empirically. Therefore, we also take the opportunity to test whether sexual size dimorphism (SSD) correlates with infestation prevalence across hummingbird species and subspecies.

2. Materials and Methods

Data were collected by Y. Oniki-Willis and E. O. Willis in June–July of 2001 and 2002 in museums in the USA. At that time, we had already learned about the biology of hummingbird lice and practiced their identification during twenty expeditions (1989–2002) to the Brazilian state of Espírito Santo to capture and band hummingbirds.

Looking for louse eggs in North American museums, we examined (i) 22,408 hummingbird specimens in the American Museum of Natural History, New York, NY, USA; (ii) 12,359 specimens in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; (iii) 9355 specimens in the Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA; and (iv) 7218 specimens in the Academy of Natural Sciences of Drexel University, Philadelphia, PA, USA.

Thus, a total of 51,340 specimens representing 721 species and subspecies of hummingbirds were examined. After excluding unsuitable specimens (e.g., damaged or misidentified; purported hybrids), infestations of 50,384 hummingbird individuals were evaluated, representing 595 taxa (i.e., species or subspecies); the number of individuals within a taxon varied from 1 to 1384. Hummingbird scientific names were updated according to the International Ornithological Committee [9].

Egg morphology enables a safe identification of lice at the generic level [30,31]; thus, our data refer to louse genera, not species. Not only morphology, but the localization of the eggs on the host body surface and localization on the feathers, are characteristics. *Trochiloecetes* lice start laying eggs on the dorsal side of the neck (nape). When infestation intensity is high, two or more eggs are attached to one feather, and the eggs are spread toward the sides of the neck, reaching even to the throat (where *Trochiliphagus* eggs are typically found). They lay smaller eggs (relative to *Trochiliphagus*) and fix them on the concave surface of contour feathers next to the calamus. Contrarily, *Trochiliphagus* lice lay larger eggs on the convex surface of feathers, also next to the calamus. Their eggs are laid on the contour feathers of the throat. When abundant, the laying area spreads to the sides of the neck and, very rarely, even to the nape. *Leremenopon* lice lay tiny eggs (relative to the former two genera) firmly glued to the rachis of body feathers. Eggs are restricted to body surface areas that are difficult to reach by the bills (depending on bill length).

The plumage of hummingbird specimens was carefully examined for louse eggs by the naked eye, using magnifiers when needed [32,33]. When necessary, fine forceps were used to collect a few individuals that fell or were attached to the skin, which were kept dry in Eppendorf vials until further identification under a stereo microscope. Only the presence or absence of each parasite genus was recorded for each host individual, because infestation intensity (the number of eggs per host individual) was not quantified.

Prevalence (the proportion of infested individuals) was calculated separately for the parasite genera found in all host taxa with 50 or more individuals (an arbitrary limit). Since prevalence is neither a host nor a parasite character but a shared character of a host–parasite species pair, we could not apply phylogenetic control for comparative analyses.

Body mass data of hummingbird taxa were obtained from the literature [34–42]. Readers should be aware that hummingbird subspecies often differ in body size and constitute, more or less, isolated epidemiological units. Despite this, our database was inconsistent in the sense that part of the host data referred to species level and another part referred to subspecies level. This was due to the lack of subspecific identification for many museum specimens as well as the lack of published data on body mass for many subspecies. Therefore, when subspecific identification was not available, we used the geographical origin of body mass data to establish subspecies identity. When that was not possible, we assumed that all species-level data referred to the nominal subspecies. This is a reasonable approximation because the nominal subspecies are typically (though certainly not always) the most widespread, abundant and best-known.

Four literature sources [36–39] provided male and female body masses separately for some of the hummingbird taxa. We regressed male body mass over female body mass, and the residuals from this regression line were used as an index of SSD.

We set out to answer the following questions.

What is the prevalence of louse infestations on different taxa of hummingbirds?

Does host sample size correlate with the observed genus richness of the parasite community hosted by each host taxa?

Does host body mass correlate with the observed genus richness of the parasite community hosted by each host taxa?

Does the prevalence of each parasite genus correlate with host body mass across host taxa?

Do the prevalence of the different parasite genera correlate with each other across host species?

Does the co-occurrence and co-absence of different parasites within the same host species (compared across host individuals) indicate any parasite associations?

Does the prevalence of each parasite genus correlate with host SSD across host taxa?

The hummingbirds analyzed here were sampled throughout most of the Americas, encompassing all major ecosystems and covering two distinct hemispheres. Consequently, habitat seasonality varies dramatically in intensity and timing throughout the study area. Further, we know very little about the molting season and the molting strategies exhibited by hummingbirds. Therefore, we cannot analyze the effects of climate, seasonality, the timing of molt, and several other relevant factors.

We did not apply data transformations to handle biased distributions of rough data. Instead, we applied Spearman rank correlations and Fisher's exact tests to explore statistical covariations between variables. All statistical tests were two-tailed.

3. Results

3.1. Prevalence of Infestations

Our data set refers to 50,384 individuals of 595 hummingbird taxa and their lice infestations. The total data set is provided in the Supplementary Materials. Overall, lice infestations were rare, most often with a prevalence of 0–10%. After excluding small samples (host $N < 50$), we found that *Trochiloecetes* was more prevalent than *Trochiliphagus*, and *Leremenopon* was much rarer, with median values of prevalence of 0.065, 0.025 and 0.000, respectively (Figure 1). *Myrsidea* was extremely rare, occurring on only one specimen out of all hummingbirds. Therefore, the genus *Myrsidea* was excluded from all analyses. Some hummingbirds, such as *Colibri coruscans coruscans* (Gould, 1846), *Colibri thalassinus* (Swainson, 1827) and *Colibri delphinae* (Lesson, 1839), carried no infestations at all, even at relatively large sample sizes (769, 370 and 250, respectively).

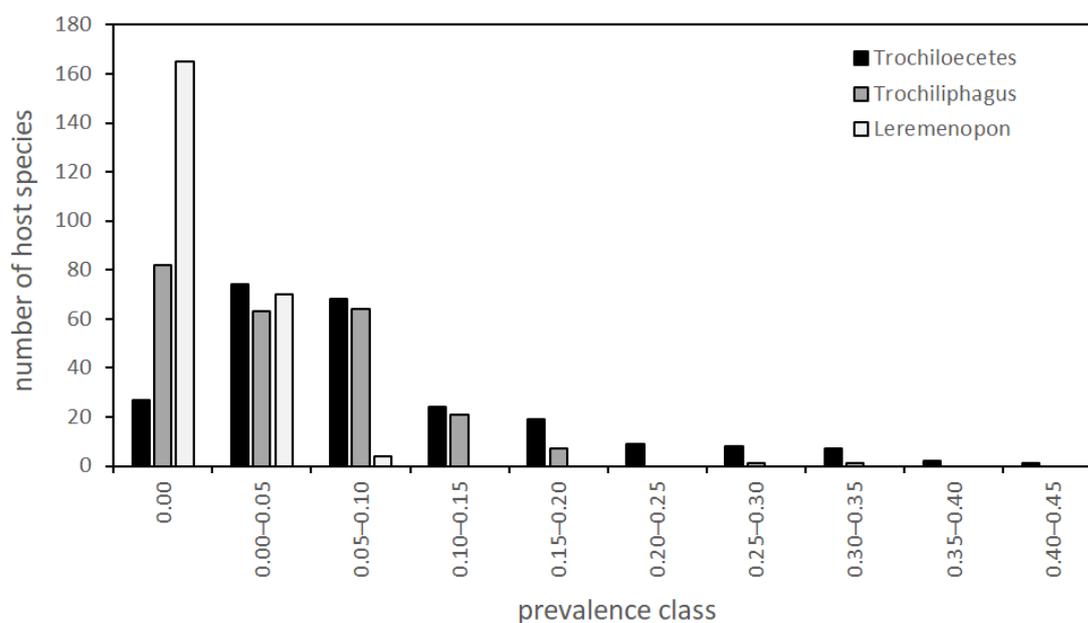


Figure 1. The distribution of 239 hummingbird taxa ($N \geq 50$ individuals) across prevalence classes, shown separately for the three parasite genera (*Trochiloecetes*, *Trochiliphagus* and *Leremenopon*).

3.2. Host Sample Size and Parasite Genus Richness

The correlation between host sample size and parasite genus richness was highly significant (Spearman rank correlation, $N = 595$, $\rho = 0.6131$, $p < 0.0001$) (Figure 2).

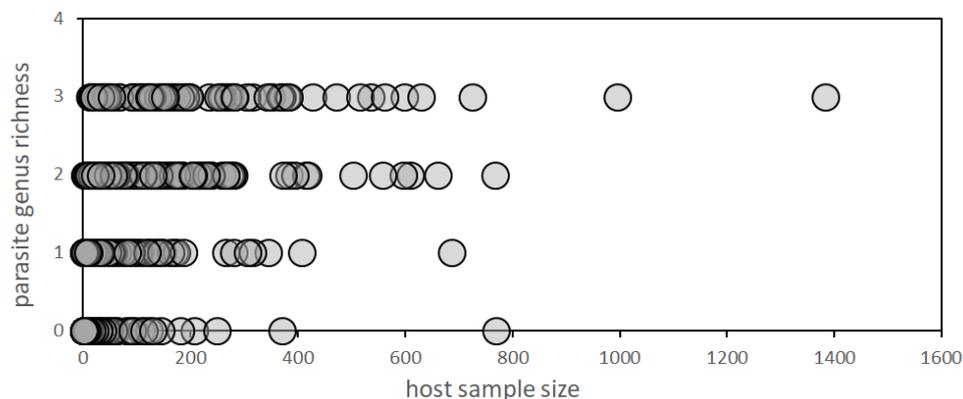


Figure 2. The relationship between hummingbird sample size and louse genus richness.

3.3. Host Body Mass and Parasite Genus Richness

Host body mass was available for 398 taxa (range: 1.9–20.2 g), and it did not correlate with louse genus richness, even if controlled for sample size bias (Table 1).

Table 1. Host body mass did not correlate with louse genus richness across hummingbird taxa (Spearman rank correlations). First, we tested the whole sample of 398 taxa. Then, to control for sample size (the number of individuals in each taxa) effects, we classified the 398 taxa into 5 classes of different sample size categories (5 ‘layers’). No significant body mass effect was detected in the whole sample or any of the 5 classes.

N Taxa	Sample Size	ρ	p
398	1–1384	0.0099	0.8436
79	1–11	0.1847	0.1032
81	12–38	0.0495	0.6609
79	39–79	−0.1419	0.2124
80	80–173	−0.1308	0.2476
79	174–1384	−0.0618	0.5885

3.4. Host Body Mass and the Prevalence of Infestations

We do not expect the sample estimates of prevalence to be biased at low sample sizes [43]; however, small samples significantly increase random noise in the estimated values. To reduce this noise in prevalence values, we removed all taxa represented by small sample sizes ($N < 50$, an arbitrary limit).

Hummingbird mean body mass data were available for 213 taxa with large sample sizes ($N \geq 50$), with values ranging from 2.2 g to 20.2 g. The prevalence of *Trochiloecetes* and *Trochiliphagus* did not correlate with host body mass. Contrarily, the prevalence of *Leremenopon* exhibited a marginally significant positive correlation with host body mass (Table 2).

3.5. Relationships between the Prevalence of Different Parasites across Host Taxa

Using the 239 hummingbird taxa with 50 or more examined individuals, we sought to determine whether the prevalence of different parasite genera correlated with one another. A highly significant positive correlation was found between the prevalence of *Trochiliphagus* and *Leremenopon* infestations, but no relationships were detected between *Trochiloecetes* and *Trochiliphagus*, nor between *Trochiloecetes* and *Leremenopon* (Table 3).

Table 2. Spearman rank correlations between host body mass and the prevalence *Trochiloecetes*, *Trochiliphagus* and *Leremenopon* across 213 host taxa ($N \geq 50$ individuals) of hummingbirds.

Variables	N	rho	p
Host body mass and <i>Trochiloecetes</i> prevalence	213	−0.0335	0.6264
Host body mass and <i>Trochiliphagus</i> prevalence	213	−0.1037	0.1316
Host body mass and <i>Leremenopon</i> prevalence	213	0.1317	0.0550

Table 3. Spearman rank correlations between the prevalence of pairs of louse genera across 239 host taxa ($N \geq 50$ individuals) of hummingbirds.

Lice Genera	N	rho	p
<i>Trochiloecetes</i> and <i>Trochiliphagus</i>	239	0.0224	0.7305
<i>Trochiloecetes</i> and <i>Leremenopon</i>	239	−0.0522	0.4215
<i>Trochiliphagus</i> and <i>Leremenopon</i>	239	0.2660	<0.0001

3.6. Parasite Co-infestations within Particular Host Taxa

A total of 31 hummingbird taxa were represented by 350 or more individuals, and 27 of them harbored both *Trochiliphagus* and *Trochiloecetes* lice. The co-infestations by these two genera were more frequent than expected in 22 cases and less frequent in 5 cases. Only 6 of these relationships were statistically significant, all of them indicating a positive interaction (Table 4). We could not carry out a similar test for the *Leremenopon-Trochiliphagus* or the *Leremenopon-Trochiloecetes* pairs of lice due to the rarity of *Leremenopon* infestations.

Table 4. The association of *Trochiliphagus* and *Trochiloecetes* lice was significantly more frequent than expected by chance in six hummingbird species.

Host Species	N	Tcet + Tpha +	Tcet -Tpha -	Tcet + Tpha -	Tcet - Tpha +	Fisher’s Exact p
<i>Archilochus colubris</i>	725	7	615	85	18	0.0294
<i>Chlorostilbon mellisugus</i>	599	6	528	37	28	0.0281
<i>Selasphorus scintilla</i>	557	4	514	31	8	0.0045
<i>Chrysolampis mosquitus</i>	428	8	361	33	26	0.0098
<i>Selasphorus platycercus</i>	394	3	370	20	1	0.0007
<i>Helianthus exortis</i>	351	2	317	32	0	0.0091

3.7. Host Sexual Size Dimorphism and the Prevalence of Parasites

Male and female hummingbird body mass data were available for 114 hummingbird taxa, and 74 of these hosts were represented by large ($N \geq 50$) sample sizes. Contrary to the interspecific prediction of the Hamilton–Zuk Hypothesis, host SSD did not correlate with the prevalence of any genus of lice (Table 5).

Table 5. Spearman rank correlations between the sexual size dimorphism (SSD) of host taxa ($N \geq 50$ individuals) and the prevalence of louse genera.

Variables	N	rho	p
Host SSD and <i>Trochiloecetes</i> prevalence	74	−0.0983	0.4045
Host SSD and <i>Trochiliphagus</i> prevalence	74	−0.0895	0.4480
Host SSD and <i>Leremenopon</i> prevalence	74	−0.1384	0.2395

4. Discussion

Our museum-based study covered 348 species plus 247 additional subspecies of hummingbirds. The species involved represent 96% of the currently known hummingbird species globally [9]; thus, this is probably the greatest coverage of a large monophyletic avian taxon for any ectoparasite ecological study. Hopefully, our descriptive results can provide baseline data for future monitoring or comparative studies. Like former authors [17],

we found that *Myrsidea* infestations were extremely rare, and therefore we excluded this genus from all analyses. Thus, we analyzed the occurrence of three genera of lice across hummingbird taxa and individuals.

Sample estimates of parasite richness are known to increase with increasing host sample size [44]. Of course, factors other than sample size must also affect parasite genus richness, as indicated by a few large samples free of infestations. Such factors need to be identified by future studies. Our data provided in Table S1 may prove helpful in future investigations to design the required sample sizes.

Contrary to former suspicions, host body mass did not correlate with parasite genus richness, even when controlled for sample size effects.

In the case of the two Rycinid genera, the prevalence of infestations did not correlate with host body mass in comparisons across host taxa. Contrarily, *Leremenopon* prevalence exhibited a weak, marginally significant positive relationship with host body mass. Admittedly, the reasons for this difference are not yet understood.

Exploring the potential relationships between the prevalence of different parasites across host taxa, we detected a strong positive correlation between *Trochiliphagus* and *Leremenopon* infestations. On the other hand, when focusing on parasite associations within the largest host samples, i.e., within particular host taxa, we found that *Trochiliphagus* and *Trochiloecetes* co-occur or are co-absent significantly more often than expected by chance in several cases.

This latter positive parasite–parasite relationship within a particular host taxon might indicate an unknown ecological relationship between louse infestations. Alternatively, it might have emerged as an artifact of our sampling method. For example, bird individuals collected soon after their last molt have had a short time to accumulate louse eggs on their feathers, while other birds collected long after their last molt have had an extended period to accumulate eggs. The timing of the last molt likely influences the egg accumulation of different lice similarly; thus, an apparent positive correlation may arise between them. As explained above, we cannot analyze the potential effects of molt timing. Therefore, future studies are needed to test whether genera of hummingbird lice truly engage in positive ecological interactions with each other, as suggested by our present results.

Finally, we analyzed the relationship between host SSD and parasite prevalence. In most hummingbirds, the male sex is heavier than the female, except for the smallest species. This avian family complies with Rensch's Rule [11,12], i.e., increasing the mean body size of the species is associated with the relatively larger size of the male sex (relative to female). We controlled for this effect by using the residuals of the female–male body size regression as an index of SSD. Using this index, we found no correlation between host SSD and the prevalence of any genus of lice. The Hamilton–Zuk hypothesis [28] describes a far more complex process than we could thoroughly examine in the present context [29]. One of its predictions, however, is not supported by our present results. At the moment, we cannot attempt to propose an explanation for this phenomenon.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d15010054/s1>. Table S1: Hummingbird louse infestation data.

Author Contributions: Conceptualization, methodology, Y.O.-W. and E.O.W.; formal analysis, L.R.; writing—original draft preparation, Y.O.-W., L.R. and L.E.L.; Writing—reviewing and editing, Y.O.-W., L.R. and L.E.L. All authors (but E.O.W.) have read and agreed to the published version of the manuscript.

Funding: Y. Oniki-Willis acknowledges financial support from the American Museum of Natural History and the Smithsonian Institution for her studies at their museums. L. E. Lopes received a research fellowship from CNPq (316960/2021-7). L. Rózsa acknowledges support from the National Laboratory for Health Security (RRF-2.3.1-21-2022-00006) and the Hungarian Scientific Research Fund (OTKA; K143622).

Institutional Review Board Statement: Not applicable.

Data Availability Statement: The rough data can be downloaded at: Table S1.

Acknowledgments: Y.O.-W. and E.O.W. appreciate help from the curators of the museums visited.

Conflicts of Interest: The authors declare no conflict of interest.

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