

Repeated Evolution of Unorthodox Feeding Styles Drives a Negative Correlation Between Foot Size and Bill Length in Hummingbirds

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Submitted ; *Accepted* ; *Electronically published*

Online enhancements: Supplemental Excel File and PDF.

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Running head: Hummingbird Foot Size and Bill Length

Keywords: Evolutionary convergence, hallux claw, functional morphology,
behavioral phylogenetics, clinging, nectar robbing.

MS type: Article

Online enhancements:

Supplemental Spreadsheet S1: Morphometric and Behavioral Data

Supplemental Figures S1–S8

Supplemental Tables S1–S14

Supplemental Text S1–S7

ABSTRACT: Differences among hummingbird species in bill length and shape have rightly been viewed as adaptive, in relation to the morphology of the flowers they visit for nectar. In this study we examine functional variation in a behaviorally related but neglected feature: hummingbird feet. We gathered records of hummingbirds clinging by their feet to feed legitimately as pollinators or illegitimately as nectar-robbers—“unorthodox” feeding behaviors. We measured key features of bills and feet for 220 species of hummingbirds and compared the 66 known “clinger” species (covering virtually the entire scope of hummingbird body size) to the 144 presumed “non-clinger” species. Once the effects of phylogenetic signal, body size, and elevation above sea level are accounted for statistically, hummingbirds display a surprising, but functionally interpretable negative correlation. Clingers with short bills and long hallux (hind-toe) claws have evolved—independently—more than 20 times, and in every major clade. Their biomechanically enhanced feet allow them to save energy by clinging to feed legitimately on short-corolla flowers and by stealing nectar from long-corolla flowers. In contrast, long-billed species have shorter hallux claws, as plant species with long-corolla flowers enforce hovering to feed, simply by the way they present their flowers.

TÍTULO: Evolución repetida de estilos de alimentación no ortodoxos conduce a una correlación negativa entre el tamaño de la pata y el largo del pico en colibríes

RESUMEN: Las diferencias en tamaño y forma de pico entre especies de colibríes han sido correctamente vistas como adaptativas, en relación con la morfología de las flores que visitan para conseguir néctar. En este estudio examinamos la variación funcional de una característica que, aunque relacionada con su comportamiento alimentario, ha sido ignorada: las patas de los

colibríes. Reunimos registros de colibríes agarrándose de las plantas con las patas para alimentarse legítimamente como polinizadores o ilegítimamente como ladrones de néctar—comportamientos de alimentación “no ortodoxos”. Medimos características claves de picos y patas en 220 especies de colibríes y comparamos las 66 especies que se sabe son “agarradoras” (cubriendo prácticamente todo el espectro de tamaño corporal de colibríes) con las 144 especies que se presume son “no agarradoras”. Una vez que se controlan estadísticamente los efectos de señal filogenética, tamaño corporal, y elevación sobre el nivel del mar, los colibríes muestran una correlación negativa sorprendente, pero funcionalmente interpretable. Las especies “agarradoras” con picos cortos y garras largas en el hálux (dedo posterior) han evolucionado, de forma independiente, más de 20 veces y en todos los clados principales. Sus patas biomecánicamente mejoradas les permiten ahorrar energía al aferrarse para alimentarse legítimamente de las flores de corola corta y al robar néctar de las flores de corola larga. Por el contrario, las especies de pico largo tienen garras del hálux más cortas, ya que las especies de plantas con flores de corola larga obligan a revolotear para alimentarse, simplemente por la forma en que presentan sus flores.

TÍTULO: A evolução repetida de estilos de alimentação não ortodoxos leva a uma correlação negativa entre o tamanho do pé e o comprimento do bico de beija-flores

RESUMO: As diferenças de comprimento e formato de bico entre espécies de beija-flores têm sido corretamente vistas como adaptativas, em relação à morfologia das flores que eles visitam para conseguir néctar. Neste estudo nós examinamos a variação funcional de um comportamento relacionado a alimentação, porém a partir de uma característica até então

ignorada: os pés dos beija-flores. Nós coletamos registros de beija-flores agarrando as plantas pelos pés para se alimentarem legitimamente como polinizadores ou ilegitimamente como ladrões de néctar—comportamentos de alimentação “não ortodoxos”. Nós medimos características chaves de bicos e pés de 220 espécies de beija-flores e comparamos as 66 espécies conhecidas como “agarradoras” (que cobre praticamente todo o espectro de tamanho do corpo de beija-flores) com as 144 espécies presumidas como “não agarradoras”. Uma vez que o efeito de sinal filogenético, tamanho do corpo, e elevação acima do nível do mar é estatisticamente controlado, os beija-flores mostram uma correlação negativa surpreendente, mas funcionalmente interpretável. Agarradores com bicos curtos e garra do hálux longa (dedo traseiro) evoluíram—independentemente—mais de 20 vezes, e em todos os principais clados. Seus pés biomecanicamente aprimorados os permitem preservar energia ao agarrarem pelos pés para se alimentar legitimamente em flores com corolas curtas e para furtar néctar de flores com corolas longas. Ao contrário, espécies com bicos longos possuem a garra do hálux mais curta, uma vez que espécies de plantas com flores de corolas longas obrigam os beija-flores a pairarem em voo para se alimentar, simplesmente pela forma como apresentam suas flores.

Introduction

It is the great diversity of forms in this family of birds which renders the study of them so very interesting. If these little objects were magnified to the size of Eagles, their structural differences would stand out in very bold relief....

—John Gould (1861, p. xxii)

Hummingbirds inhabit nearly every part of the Americas, at least seasonally, from sea level to tree line and beyond. In fundamental ways, all ~340 species of the hummingbird family (Trochilidae) are so similar that any rural child from Alaska to Tierra del Fuego would likely know on sight that any hummingbird—from anywhere—was indeed a hummingbird. Nonetheless, some species weigh less than 2 grams and others more than 20; some have short bills, some long, some straight, some curved; some are plain, and others display a rainbow of colors in their plumage. In some species, females and males differ greatly in plumage (Bleiweiss 1997; Colwell 1989; Gould 1861; Parra 2010) and size (Colwell 2000); in others, the sexes are indistinguishable.

Have hummingbirds simply evolved elaborate variations on a successful theme? Certainly, some key features are universal in the family and known in no other birds, including their remarkable adaptations for prolonged hovering (Altshuler and Dudley 2002) and nectar extraction (Rico-Guevara et al. 2019; Rico-Guevara and Rubega 2011). In contrast, differences among species in bill length and shape have long been rightly viewed as adaptive, co-evolved responses to—or causes of—the morphology of the flowers they visit for nectar (Maglianesi et al. 2015; Stiles 1981; Temeles and Kress 2003; Weinstein and Graham 2017). Likewise, differences in foraging tactics set species apart in clearly adaptive ways (Altshuler et al. 2004b; Feinsinger and Colwell 1978; Rodríguez- Flores and Arizmendi Arriaga 2016; Sargent et al.

2021), and allometry in wing size tuned to declining air density allows hovering flight in species resident at higher elevations (Altshuler et al. 2010; Altshuler et al. 2004a; Feinsinger et al. 1979; Skandalis et al. 2017).

Fascination with their unique and conspicuous adaptations for flight and nectar feeding and the allure of hummingbird plumage and courtship behavior have distracted researchers from functional variation among hummingbird species in a neglected feature of their bodies: their tiny feet and claws. Little has been added to our understanding of hummingbird feet in the century and a half since (Gould 1861), p. xxii) wrote:

Nothing yet has been said respecting the legs and feet. Diminutive as they are, they will be found to be very diversified. In some instances...the toes are very diminutive, and are furnished with equally small, rounded nails; in others all the toes, particularly the hinder one, are greatly developed and armed with long, curved, and extremely sharp, spine-like claws. This latter form is admirably adapted for clinging to the petals of flowers, a habit common to many members of the family, which not only settle upon, but thrust their spiny bills through the bell-shaped flowers.

The notion that these "footless" birds (Order Apodiformes) use their feet and toes solely for upright perching while at rest (and for grooming) accurately describes the behavior of many species, but it is clearly false for others, as Gould first pointed out and many others have since confirmed (Supplemental Spreadsheet S1).

We gathered all available records of clinging to feed and other “unorthodox” hummingbird feeding styles from individual species accounts, assemblage studies, and other sources and measured key morphological features in specimens of 220 species of hummingbirds (Supplemental Spreadsheet S1). We show that, once the confounding effects of phylogenetic signal, body size, and elevation above sea level have been accounted for statistically, hummingbirds display a surprising but functionally interpretable pattern—a morphological

paradox that defies the expectation of simple variations on a theme. Species with longer bills have smaller feet, and species with shorter bills have larger feet (see the graphic overview in Fig. 1).

[Figure 1 near here]

Hummingbird Feeding Styles

The role of bill length and curvature. The key to understanding variation among hummingbird species in the use of their feet while feeding from flowers lies squarely in the coevolved morphologies of flowers and hummingbird bills. Among the 220 species examined for this study, bill length—measured along the dorsal surface of the bill, whether curved or straight—varied from a minuscule 7 mm (exposed culmen), for the aptly-named *Ramphomicron microrhynchum* (purple-backed thornbill), to 88 mm for the remarkable *Ensifera ensifera* (sword-billed hummingbird) (Supplemental Spreadsheet S1). In principle, a hummingbird can feed *legitimately* (through the mouth of the corolla [Inouye 1980]) and extract nectar from any corolla shorter than the length of its bill, plus the effective reach of its tongue (Rico-Guevara 2017).

Thus, on one hand, short-billed birds cannot drain long-tubed flowers, legitimately, simply because they cannot reach all of the nectar (Feinsinger 1976; Rico-Guevara et al. 2019; Snow and Snow 1972; but see Ewald and Williams 1982; Rengifo et al. 2006). On the other hand, strong arguments from functional morphology imply that long-billed birds are less efficient than short-billed birds at the extraction of nectar from short-tubed flowers (Rico-Guevara et al. 2019, 2021; Temeles 1996; Temeles et al. 2002), as first suggested by Snow and Snow (1972), Stiles (1975), and Wolf et al. (1976). Moreover, in many cases, short-billed birds aggressively exclude long-billed species from defended feeding territories, protecting the nectar

sources that short-billed birds are most capable of exploiting (Feinsinger and Colwell 1978; Skandalis et al. 2017; Snow and Snow 1980), although there are exceptions in which longer-billed species, particularly males with weaponized bills, dominate shorter-billed species (Rico-Guevara et al. 2019). The net result is a manifest correlation between the corolla morphology of flowers pollinated by hummingbirds and the length of their bills (Fig. 1, photographs *a* and *b*) (Betts et al. 2015; Maglianesi et al. 2014; Snow and Snow 1980; Weinstein and Graham 2017; but see Missagia and Alves [2018]).

Bill curvature complicates this seemingly simple relationship. Many hummingbirds with decurved bills (*e.g.*, *Eutoxeres* spp. and many other hermits [Fig. 1, photograph *h*], but also non-hermits, such as *Eulampis* spp.) feed principally from flowers with similarly curved corollas, which tend to exclude or discourage straight-billed birds. Hummingbirds with curved bills, however, cannot feed efficiently (or sometimes, at all) from straight-tubed flowers (Rico-Guevara et al. 2019; Temeles et al. 2009).

Unorthodox feeding styles: Base-workers and secondary nectar robbers. In our terminology, any feeding style other than feeding legitimately, while hovering, is “unorthodox.” A pervasive form of unorthodox feeding involves the *illegitimate* extraction of nectar from long-tubed flowers by short-billed hummingbirds—by any means other than through the throat of the corolla. This activity, of course, does nothing to pollinate the plant and imposes an energetic cost on both the plant and on legitimate visitors, by depleting nectar (but may or may not affect plant fitness [Maloof and Inouye 2000]).

In some cases, a hummingbird simply inserts its bill through natural openings near the base of the flower (called a “base worker” by Weaver [1956] and Inouye [1980; 1983]). For example, in flowers of the genus *Lobelia* (Campanulaceae), the petals are joined into a tube

distally, but remain separate basally. Through these interstices—especially in long-corolla species—short-billed species take nectar quite freely, often while clinging horizontally, vertically, or even upside down. In a striking example, on the central coast of Chile, *Sephanoides sephaniodes* (green-backed firecrown, with a 22 mm bill), steals nectar from the 40 mm corollas of *Lobelia excelsa*, which is obligately pollinated by the long-billed *Patagona gigas* (giant hummingbird, with a 38 mm bill) (RKC personal observation; Wagner [1946] reports another example).

In other cases, short-billed hummingbirds (“secondary nectar robbers,” in the terminology of Inouye [1980]) take nectar from the base of long corollas through openings made by other birds that have forced entry into the nectary chambers of long-tubed flowers (Irwin et al. 2010). In the tropical highlands, the passerine birds known as flowerpiercers (*Diglossa* spp.) rob nectar from hummingbird-pollinated flowers through slits in the corolla that they make with their own, chisel-like lower mandible (Rojas- Nossa et al. 2016; Schondube and Martínez del Río 2003). Hummingbirds may then use the same slits to extract floral nectar they otherwise could not reach (Arizmendi 2001; Colwell 1973; Kjonaas and Rengifo 2006; Pelayo et al. 2011; Wolf 1969). Likewise, floral perforations made by the passerine, *Coereba flaveola* (bananaquit), are used by several hummingbirds (Borrero and Ignacio 1964; Ingels 1976; Supplemental Spreadsheet S1 details additional records.)

Unorthodox feeding styles: Primary nectar robbers. Some hummingbird species make their own perforations in the base of intact flowers, by forcing the bill through corolla tissue—“primary nectar robbers,” in the terminology of Inouye (1980)—either while clinging (Fig. 1, photograph *f*) or on the wing (Fig. 1, photograph *g*) (Gould 1861, p. xv; Skutch 1951; Skutch 1973; Skutch 1940). Supplemental Spreadsheet S1 details many records of primary nectar

robbers. It has been suggested that, in some species, specialized bill morphology may be involved (Ornelas 1994; Remsen et al. 2015; but see Rico-Guevara et al. 2019). Proving that such hummingbirds make their own perforations in corollas, rather than using existing ones made by insects or other birds (Igić et al. 2020) is not easy. But before-and-after observations of individual flowers visited by nectar thieves offer unequivocal evidence (Boehm 2018; Colwell 1973; Snow and Snow 1980).

The orthodox feeding style: Legitimately, on the wing. Most hummingbirds readily use any suitably stable object to perch horizontally while feeding on flowers, legitimately, as long as the position of the perch permits more or less the same approach to the flower that would be taken while hovering. For our purposes here, we do not consider perching horizontally to feed to be “unorthodox.” However, the great majority of hummingbird-pollinated flowers are “presented” by plants—often oblique, drooping, or pendent from a flexible pedicel, with the corolla throat facing down (Fig. 1, photographs *a*, *b*, and *f*)—in such a way that legitimate access to the flower is difficult or impossible from horizontal perches, even if available. In this way, most plants force hovering on their legitimate hummingbird visitors (Feinsinger and Colwell 1978; Fleming and Muchhala 2008; Miller 1985; Snow and Snow 1980; Stiles 1981). Non-pollinating birds and mammals seeking nectar or pollen have presumably provided strong selection for these floral resources to become as inaccessible as possible to non-hummingbirds (Stiles 1981), but there is also some evidence that flexible pedicels enhance pollen deposition on visiting hummingbirds (Hurlbert et al. 1996).

Clingers vs. non-clingers

With the exception of piercing flowers to feed illegitimately on the wing (Fig. 1, photograph *g*), all the unorthodox feeding styles detailed above require the use of the legs and feet to grasp a

substrate (*e.g.*, a flower, bract, pedicel, leaf, petiole, branch, or stem) sideways (Fig. 1, photographs *c, f*, and *h*) or hanging upside down (Fig. 1, photograph *d*) during the act of feeding. Following Gould (1861) and others, we refer to this behavior as *clinging*. We call hummingbirds known to perform it *clingers*, and those species not known to do so as (presumed) *non-clingers*. All hummingbirds *perch* on horizontal substrates to rest and nearly all (Carpenter 1976) to sleep. In the terminology of vertebrate functional morphology, both perching and clinging are forms of *grasping*, which enjoys its own substantial literature (Sustaita et al. 2013). Here we are concerned exclusively with clinging to feed.

As detailed in *Methods*, in this study we relied on museum specimens as well as living individuals for measurements of hummingbirds. Although the bird foot is a complex, integrated unit with a multitude of parts, we have limited our quantitative analysis to four key foot elements that can be easily and accurately measured in both living birds and museum study specimens (round-skins)—tarsometatarsus (tarsus) length, hallux length, hallux claw chord, and middle-toe claw chord (Fig. 2).

[Figure 2 near here]

The literature on avian grasping biomechanics has little to say about hummingbirds, but studies of other birds offer some guidance on which features of the hummingbird hindlimb are most likely differ between clingers and non-clingers. We review this literature in depth in Supplemental Text S1 (*The functional morphology of clinging*) and illustrate key principles in Fig. S1 (*The mechanics of clinging in hummingbirds*). The upshot is that relatively longer toes (Backus et al. 2015) and claws (Norberg 1986; Winkler and Bock 1976) (Fig. 2) can expand the avian foot span, minimizing the horizontal forces that would otherwise pull a clinging bird off the substrate, thus reducing the muscle forces required to oppose them (Fig. S1, panels G and H).

In contrast, relatively shorter tarsi (Fig. 2) enhance the mechanical advantage of the ankle flexors that act to hold the body close to the substrate (Leisler and Winkler 1985; Moreno and Carrascal 1993; Norberg 1979; Zeffer et al. 2003; Zeffer and Norberg 2003), potentially reducing the cost of clinging (Fig. S1, panels E and F). Thus, before examining the data, we predicted that clingers would have relatively longer toes and claws, but shorter tarsi, than non-clingers.

Methods

Morphological Data

For this study, we pooled three independently gathered (by RKC, AR-G, and GMY) datasets comprising 1154 museum specimens and 404 field captures, representing 220 of the approximately 340 recognized species of hummingbirds. (All records, with the source of each specimen, are available in the Harvard Dataverse repository at <https://doi.org/10.7910/DVN/THDJCI>). For each specimen, we measured *bill length* (exposed culmen), *tarsus length*, *hallux-claw length* (chord of digit I claw), and *wing length* (chord) (as defined by Baldwin et al. [1931]), and recorded sex and field weight from museum specimen tags and from most field captures (Fig. 2, Supplemental Spreadsheet S1, and Harvard Dataverse repository). Sample sizes ranged from a single specimen, for each of 10 very rare species, to more than 100 specimens for a few common species. Thus, the sample size for the full dataset in this study is properly viewed as $n = 220$ species, with variable precision (which we estimate and take into account; see below) for individual data points, but with no reason to expect any directional biases from different numbers of specimens measured, per species.

For a subset of 103 species, RKC also measured *middle-toe claw length* (chord of digit III claw, Fig. 2), one specimen per species, disregarding sex. For a subset of 155 species, GMY also

measured *hallux toe length* (digit I), for one-to-35 specimens per species, disregarding sex (Fig. 2, Supplemental Spreadsheet S1, and Harvard Dataverse repository).

Hummingbirds display a clear pattern of allometry for sexual size dimorphism (Rensch's rule), with females larger than males in small species and males larger than females in large species (Colwell 2000). In this study, we rely, in the first instance, on intersexual averages (the average for all specimens, disregarding sex). To assess the possible impact of sexual dimorphism on results, we repeated key analyses with females-only (209 species) and males-only (204 species) data subsets. Raw species morphometric means for intersexual averages, for females, and for males appear in Supplemental Spreadsheet S1.

Although we recorded field weights from specimen museum tags or in the field for nearly half of the individuals measured, such records are often considered unreliable, because of substantial diurnal and seasonal changes in live body mass (Carpenter et al. 1983) and the difficulty posed by weighing such tiny birds accurately in the field. Museum specimen tags sometimes have crude estimates, in even grams, recorded by early collectors (*e.g.*, M. A. Carriker, in the 1930s), who probably lacked accurate scales or even had none at all. Thus, for consistency and repeatability, we opted to rely primarily on published species weights (Dunning 2007; Schuchmann 1999) (Supplemental Spreadsheet S1), using the museum specimen tag weights and live field weights in our dataset only to check for outliers and errors, to estimate measurement error (as weighted, among-specimen variance, within species [Warton et al. 2006]), and to provide data for a few species lacking credible weights—or any weights—in the literature. For separate-sex analyses, we relied on mean museum specimen tag weights and field weights from our own dataset, since published, sex-specific weights were not available for many species for which we nonetheless had sex-specific morphometric data.

Elevation Above Sea Level

All hummingbirds live on an extraordinarily tight energy budget (Powers and Conley 1994; Suarez 1998), but the challenges of life at higher elevations—with reduced air density, lower partial pressure of oxygen, and colder climates—are extreme. These conditions have produced both physiological (Altshuler and Dudley 2002; Groom et al. 2018; Groom et al. 2017; Projecto-Garcia et al. 2013) and morphological (Altshuler et al. 2004a; Feinsinger et al. 1979) adaptive responses in hummingbirds.

Clinging to feed from flowers saves energy, compared with hovering to feed (Carpenter 1976; Stiles 2004; Wolf et al. 1975), so that selection for this behavior and for the morphological features that facilitate it would be expected to be stronger at higher elevations. While the amount of energy saved by clinging has never been measured, it is reasonable to assume it is significant, given the extreme energy demands of hovering. Indeed, several species of the Coquette clade—comprised mostly of Andean species—are notable for their strong feet (Stiles 2008), and a few species of this group that live at very high elevations even walk or hop on the ground between food plants (Fig. 1, photograph *e*) (Carpenter 1976; Miller 1985; Schulenberg and Sedgwick 2020). With these facts in view, we recorded an approximate mean elevation for each species (Supplemental Spreadsheet S1), for use in disentangling the causes of clinging behavior. See Supplemental Text S2: *Methods: Elevation*, for details of our approach to estimating an elevation for each species' geographic range.

Behavioral Data: Feeding Styles

As far as we are aware, all species of hummingbirds feed legitimately, on the wing—either sometimes, or always—including such notorious clingers as *Eutoxeres* (sicklebills) (Boehm et al. 2022) and *Schistes* (daggerbills) (Agnes Dellinger, *pers. comm.*). We searched the literature,

online resources, and our own field notes for records of individual hummingbird species that also feed in one or more of the following, unorthodox ways: (1) feeds from the ground; (2) feeds legitimately, while clinging; (3) feeds using existing openings in flowers, while clinging; (4) pierces flowers to feed, while clinging; (5) feeds on the wing, through existing pierces; (6) pierces flowers to feed, on the wing (Fig. S2). In addition to literature citations and personal observations by the authors and other informants, we searched for text references to unorthodox feeding styles in del Hoyo's authoritative species accounts (Del Hoyo et al. 2018) and examined every photograph and video in each of del Hoyo's comprehensive online species accounts (birdsoftheworld.org, as of August 2020) for photographic evidence of unorthodox feeding, finding many additional instances in this way (Supplemental Spreadsheet S1). We considered a single, unambiguous instance of each unorthodox feeding style to be definitive. We elected not to rely on citizen-scientist photographs (*e.g.*, eBird) for this study, because of the necessity for authoritative identifications.

In the absence of information that a particular species uses one or more of the unorthodox feeding styles we defined, we were obliged to assume that the species feeds legitimately, on the wing, and in no other manner. Thus, all such species were treated as presumptive “non-clingers” for analysis. Of course, additional unorthodox feeders may well lurk, undocumented (or documented after our survey), among the species that we have been obliged to classify as non-clingers. However, many well-studied species (including all ~15 hummingbird species that commonly occur north of Mexico) have, to our knowledge, never been documented to cling while feeding. Hummingbird species vary enormously in the intensity with which they have been studied, depending upon population density, range size, and accessibility, but it did not prove feasible to assign confidence levels to our feeding style assignments. In our analysis of the

evolutionary origins of clinging (*Results*), we take steps to assess the sensitivity of results to this source of uncertainty.

For analyses contrasting the morphology and evolution of clingers versus non-clingers, we pooled the four feeding styles that require clinging (the first four styles in Fig. S2) as “clingers.” Because we are primarily interested in clinging behaviors, for analysis we combined “feeds on the wing, through existing pierces” and “pierces flowers to feed, on the wing” into a single category: “feeds through pierces on the wing,” while recording distinctions for future study in Supplemental Spreadsheet S1.

Phylogenetic Data and Analysis

Estimating phylogeny, with uncertainty. We based our phylogenetic analyses on the molecular study of McGuire et al. (2014), who published a single tree for 284 species, based on 436 exemplars. Phylogenies are, inevitably, estimates subject to uncertainty, and molecular phylogenies are no exception. To account for this uncertainty and assess its effect on inferences, we applied the method of Rangel et al. (2015), which requires a large number of plausible, alternative trees. We obtained the sequence alignment matrix from J. McGuire (personal communication), which allowed us to closely approximate the analysis of McGuire et al. (2014). With these data, we used Mr. Bayes v. 3.2 (Ronquist et al. 2012) to produce a posterior random sample of 1000 alternative trees, after discarding the first 25% of trees as burn-in. The dataset was partitioned by gene, and substitution models were assigned to partitions as described by McGuire et al. (2014) in their supplementary information. As a check, we compared a consensus tree from our analysis (Fig. S3A) with the published tree of McGuire et al. (2014), finding only very minor topological differences. For each morphological variable in Supplemental Spreadsheet S1, and for each univariate, bivariate, or

allometric analysis, a set of 100 phylogenetic trees was drawn at random from the set of 1000, to further reduce any effect of sampling error or idiosyncratic trees.

Data for the 220 species of the full dataset encompassed 12 species not included in the McGuire phylogeny. Using the method of Rangel et al. (2015), we placed these “phylogenetically uncertain taxa” (PUTs), at random within the “most derived consensus clade” (MDCC) that unequivocally contains each PUT, without creating polytomies, independently, in each of the 100 alternative phylogenies used to generate the distribution of PGLS residuals for each morphological variable and for each statistical analysis. These 12 species and the literature authorities for assigning each to its MDCC appear in Table S1.

The phylogeny of feeding styles. We estimated the number of independent origins of clinging to feed (and putative reversals to exclusively hovering to feed), in the first instance, by applying simple parsimony analysis (Maddison and Maddison 2019) to infer ancestral character states, based on the 220-species Bayesian consensus tree as a cladogram with arbitrary branch lengths. We performed additional character evolution analyses using the R package `phytools` (Revell 2012) to assess two rate-based models, based on stochastic character mapping (Bollback 2006; Huelsenbeck et al. 2003): ARD (allowing for different rates for the hover-to-cling and cling-to-hover state changes) and ER (which assumes equal rates for both transitions). These analyses included 208 taxa, as opposed to 220 in the parsimony reconstruction, as the 12 PUTs could not be included for lack of branch lengths. To display results from the `phytools` analysis, feeding style was mapped onto the tree using the `make.simmap` function, using 100 simulations.

Statistical Methods

Accounting for phylogenetic autocorrelation: Phylo-filtered scores. For each morphometric character (weight, bill, wing, tarsus, hallux claw, and middle-toe claw; Fig. 2), we extracted

phylogenetic generalized least squares (PGLS) scores (regression residuals) (Paradis 2011; Rohlf 2001), for each of the 220 species in our dataset (103 species for middle-toe claw), based on \log_{10} of intersexual arithmetic means among specimens. The PGLS analyses were carried out using code written by TFR in the Delphi programming language, an implementation of Object Pascal (details in the Harvard Dataverse repository). For each character, we repeated the PGLS analysis for each of 100 alternative phylogenetic trees, randomly chosen from the pool of 1000 trees (see *Phylogenetic data and analysis*, above). Instead of relying on phylogenetic mixed models for inference, we used the means among the 100 scores—one from each phylogeny—for each character and each species for further analysis, to allow partitioning of the PGLS scores by feeding style, clade, elevation, or other variables, to allow identification of outliers, and to make the mean scores accessible for others to explore (Supplemental Spreadsheet S1). We repeated the entire process, separately, for females (209 species) and for males (204 species).

To simplify the presentation of results, we henceforth refer to these mean morphometric trait scores, statistically filtered to remove *only* the effects of phylogenetic autocorrelation, as *phylo-filtered scores*. The concept of “filtering out” the effects of autocorrelation is a familiar metaphor in spatial statistics, which shares conceptual and mathematical foundations with PGLS (Diniz-Filho and Bini 2005; Griffith 2003; Griffith and Peres-Neto 2006; Kühn et al. 2009). We used phylo-filtered scores for allometric analyses to estimate and interpret the scaling of the linear morphometric characters (bill, wing, and foot traits) with body size, comparing the allometry of clingers and non-clingers.

Our implementation of PGLS assumes a Brownian motion model of trait evolution and phylogenetic branch lengths proportional to molecular substitutions. Using the R (R Core Team

2021) packages `geiger` (Harmon et al. 2008) and `phytools` (Revell 2012), we assessed the validity of the assumption of Brownian motion for each morphometric character, separately, by computing an estimate of Pagel's lambda (Freckleton et al. 2002; Pagel 1999), with and without correction for measurement error, based on the consensus tree that emerged from our phylogenetic analysis.

Accounting for phylogenetic autocorrelation, body size, and elevation: Triple-filtered scores.

We accounted for phylogeny, body size, and elevation above sea level—together—in the PGLS framework, just as detailed above, to yield residual scores for each character and each species, averaged over 100 phylogenies, repeated for males and females, separately. Extending the filtering metaphor, we henceforth refer to these mean morphometric trait scores as *triple-filtered scores*. We used these scores for (1) univariate comparisons between clingers and non-clingers, for each character, individually, and for (2) bivariate analyses to assess relations between pairs of linear traits (bill and foot characters) for clingers *vs.* non-clingers. The rationale for filtering out any influence of elevation above sea level on PGLS scores for morphology was to isolate direct relations between clinging behavior and morphology from any confounding effects of elevation on both. In a separate analysis, we assess the prevalence and morphological correlates of clinging as a function of elevation.

For bill and foot characters, we estimated error due to phylogenetic uncertainty (Rangel et al. 2015) as the weighted average of the within-species sample variance, among 100 alternative phylogenies, of triple-filtered PGLS residuals for each species in our dataset, using Eq. 31 of Warton et al. (2006).

Univariate comparisons between clingers and non-clingers. For univariate morphological comparisons between bill and foot-variables of clingers versus non-clingers (using triple-

filtered PGLS scores), we computed effect size (with 95% confidence intervals) as Hedges' g_p , with pooled standard deviation in the denominator (Cumming 2013; Goulet-Pelletier and Cousineau 2018) (details in the Harvard Dataverse repository). We rely on Cohen's (1992a) characterization of small ($g_p = 0.2$), medium ($g_p = 0.5$) and large ($g_p = 0.8$) effect sizes for comparison of sample means. For completeness, we also computed two-sample t -tests (or Welch tests for unequal variances, when necessary, after comparing variances with an F -test) on triple-filtered PGLS scores, applying false discovery rates (FDR) to control for multiple comparisons (details in the Harvard Dataverse repository). See Supplemental Text S3, *Effect size vs. null hypothesis significance tests (NHSTs)* for a discussion of our approach to inference. We assessed the impact of statistical outliers on these analyses (and on bivariate analyses, below) by comparing results for all data to corresponding results excluding significant outliers, as determined by iterative Grubbs' tests (graphpad.com/quickcalcs/Grubbs1.cfm).

Bivariate relations between traits, including allometry, for clingers vs. non-clingers. To assess relationships between pairs of morphometric traits, following the authoritative recommendations of Warton et al. (2006), Smith (2009), and Freckleton (2009), we implemented Standardized Major Axis (SMA) line-fitting ("Reduced Major Axis," RMA, *sensu* McArdle [2003] and Smith [2009]). We estimated SMA slopes and SMA elevations (height above the X -axis), with 95% confidence intervals, for pairs of morphological variables, using tools in the R package `smatr3` (Warton et al. 2012), adjusting for measurement error in both variables (Warton and Weber 2002), as estimated based on our original measurements from multiple specimens of most species (see Supplemental Text S4, *Methods: Measurement error*, and examples in the Harvard Dataverse repository). For allometry (body size vs. other variables), we analyzed phylo-filtered data; for pairs of morphological variables not involving

body size, we analyzed triple-filtered data. We computed SMA slopes for clingers and for non-clingers, with and without outliers. We compared the SMA slopes for clingers vs. non-clingers using tools in the `smatr3` package (Warton et al. 2012). For each pair of morphological variables, we repeated all analyses for males and females, separately.

For allometric analyses, we treated body size just as we did each of the other morphometric traits in this study—as a co-equal element of an integrated phenotype (Murren 2012), rather than as an independent explanatory variable, as in OLS regression. (In the *Discussion*, we explain how body size can respond to selection on other characters.) For comparability with studies that report only OLS slopes for allometric relations (*e.g.*, Bennett 1996), we report OLS slopes, adjusted for attenuation due to measurement error in body mass by the "method of moments," as implemented in `smatr3` (Warton et al. 2012).

For each bivariate relation, we report the Pearson product-moment correlation coefficient r , with 95% confidence intervals, as the appropriate index of effect size, relying on Cohen's (1992a) characterization of small ($r = 0.1$), medium ($r = 0.3$) and large ($r = 0.5$) effect sizes for correlation. For completeness, we also report traditional P -values, together with false discovery rates (FDR) for families of related results, to account for multiple comparisons.

Results

Feeding styles

Feeding style records. Of the 220 species in the full dataset, we found records of unorthodox feeding styles for 76 (Supplemental Spreadsheet S1), of which 66 are known clingers. (The other 10 unorthodox feeders feed through pierces, on the wing.) Half of these species are reported to use more than one of the six unorthodox feeding styles that we scored. Each species

was assigned to a single category, for analysis and graphic presentations, as shown in Fig. S2 and explained in its caption.

The phylogeny of feeding styles

Parsimony analysis. Figure 3 maps the 76 species for which we have records of unorthodox feeding on a modified consensus phylogenetic tree from our re-analysis of McGuire's (2014) data, using simple parsimony (Maddison and Maddison 2019). Based on the data on unorthodox feeding available at the time of our investigation, the parsimony analysis revealed 26 independent origins of clinging behavior.

[Figure 3 near here]

On one hand, taking our mapping (Fig. 3) at face value may overestimate the number of independent origins of clinging to feed, if additional clingers unite species or clades of documented clingers. On the other hand, undocumented clingers might very well represent additional instances within clades already designated as clingers, leaving the estimate of independent origins unchanged, or entirely new instances. To assess the sensitivity of the parsimony analysis (Fig. 3) to the overestimation of independent origins, we modified the character mapping so that any two instances of clinger origination separated by only one subtending node were assumed to have clingers as their most recent common ancestor, thus designating a single origin of clinging behavior for both species (or both clades) of each such pair (Fig. S3). This exercise had virtually no effect, reducing the initial 26 independent origins only by 2, to 24. Every named clade of hummingbirds (except for the small—four-species—Topaz clade, with only one species on our reconstructed phylogeny) nonetheless had one or more independent origins of clinging. The Coquette clade clearly includes the largest number of clingers (a fact noted by Carpenter [1976] and Stiles [2008]), and may have had a single, basal

origin of clinging behavior, according our analysis (Fig. 3). In a later section, we assess the impact of the Coquettes on our overall results.

Evolutionary rates analysis. Of the two models we tested, the ER model (which assumes equal rates for the hover-to-cling and cling-to-hover state changes) received a lower AIC score than ARD (allowing for different rates for the two transitions) as well as a higher AIC weight and was therefore used in the simulation analysis. The results from the ER analysis were almost entirely concordant with the simple parsimony analysis, yielding 27 total putative origins of clinging, all but one of which was supported by parsimony analysis, as well (Fig. S4).

Measurement error variance, Pagel's lambda, and phylogenetic error variance. Measurement error variance (Supplemental Text S4), estimated as a weighted average of the sample variance, among individuals, within species, for each character (Warton et al. 2006), proved to be modest in relation to natural (evolutionary) variance among species (Table S2). As a percentage of total variance, measurement error variance averaged about 5%. Because error bias in SMA slopes depends on the ratio of between error variance in X and Y , the effect on slopes proved even more minor (Supplemental Text S4).

Computation of Pagel's lambda confirmed a high level of correspondence with the assumed Brownian motion model of trait evolution. All morphometric characters in this study (Supplemental Spreadsheet S1) express a significant phylogenetic signal ($P < 0.0001$), with Pagel's lambda close to 1 (mean among characters = 0.94, adjusted for measurement error; mean = 0.92 unadjusted, Table S2).

The impact of phylogenetic uncertainty (Rangel et al. 2015) on the analysis of bill and foot characters proved to be negligible, despite visible effects when results of all 100 phylogenies are plotted together (see *Feeding styles and the negative correlation between bill*

length and hallux claw). The estimated error variance of triple-filtered PGLS scores for each character, as a proportion total phylogenetic variance (variance among PGLS species means) for the character, averaged less than one-tenth of one percent (Table S2).

Univariate Analyses: Bill Length and Foot-Variables

With body size, phylogeny, and elevation above sea level filtered out (triple-filtered data), we compared clingers vs. non-clingers for bill length and foot-variables (tarsus, hallux claw, and middle-toe claw) (Table S3). As predicted, based on the natural history of unorthodox feeding in relation to floral resources, clingers have substantially shorter bills than non-clingers (effect size $g_p = 0.462$, without outliers—nearly half a standard deviation, a "medium" effect size—and a highly significant difference, $P = 0.002$, by NHST criteria). As predicted, based on fundamental principles of functional morphology (Fig. S1 and Supplemental Text S1), clingers have longer hallux claws than non-clingers ($g_p = 0.485$, $P = 0.001$, no outliers). However, contrary to functional expectations that clingers have shorter tarsi (Fig. S1 and Supplemental Text S1), clingers do not differ from non-clingers in the length of their tarsi. Middle-toe claws do not differ in length, between clingers and non-clingers, but are significantly less variable among clingers than among non-clingers.

Bivariate Relationships: Bill Length and Foot-Variables

In principle, the expected relation between one linear morphological character plotted against another, with the effects of phylogeny and body mass already filtered out, for both characters, need not produce anything but a statistically random pattern, as random deviations from a common shape would be uncorrelated. However, to the degree that the two characters are functionally integrated, the PGLS residuals for the two variables should, in general, be expected to show positive covariation (Peiman and Robinson 2017): a species with an unusually large

foot (for its body mass and phylogenetic placement) might require both a unusually longer tarsus and longer toes and claws, whereas a species with an unusually small foot would likely have smaller versions of these characters. In contrast, morphological characters related indirectly by correlational selection on distinct phenotypic features may covary either positively or negatively.

Figure S5 and Table S4 show the patterns of covariance (or lack of it) between PGLS residuals for pairs of traits likely to be involved in clinging to feed in hummingbirds, for triple-filtered data. In Fig. 4, we summarize these results diagrammatically. For all species pooled (Fig. 4A), PGLS residuals for the three foot-variables are inter-related by positive SMA slopes. The implication of this pattern is that foot proportions are generally constrained, but that some species deviate from the overall pattern in the direction of larger feet, while others have smaller-than-expected feet. The negative slope between bill and hallux claw stands out as the only relation between foot and bill with a detectable effect size, for all species considered together (Fig. 4A). For clingers (Fig. 4B), this negative relation, alone, dominates the pattern of bivariate relations, and surely drives the corresponding relation for all species pooled, given the absence of any detectable relation between bill and hallux claw among non-clingers (Fig. 4C).

[Figure 4 near here.]

Clinger foot PGLS residuals (Fig. 4B) have undetectable levels of covariation among themselves, suggesting homogeneous proportions among these traits, deviating little from a common pattern, despite multiple, independent origins of clinging behavior. The pattern of covariation among the three foot-variables for non-clingers (Fig. 4C) mirrors (and no doubt drives) the corresponding relations for all species pooled (Fig. 4A), apart from the relation between bill and hallux claw length. The positive relations between bill and tarsus, and between

bill and middle-toe claw among non-clingers suggest a further level of phenotypic integration between bill and foot in species that feed without clinging, independent of body size and phylogeny.

Feeding styles and the negative correlation between bill length and hallux claw. The univariate results (Table S3) and the negative relation between bill length and hallux claw (Fig. 4AB, Fig. S5B, and Table S4) reveal the primary functional basis for clinging in unorthodox feeders—at least among the foot characters we have considered. Clingers tend to have relatively longer hallux claws than non-clingers, but do not differ from non-clingers in tarsus length.

To explore the key relation between bill and hallux claw result at a deeper level, in Fig. 5 we expand Fig. S5B to display feeding styles, individually, for each of the 220 species of hummingbirds in our study (Supplemental Spreadsheet S1). The legend in the upper right corner indicates the color code for each style, and the miniature plot in the lower left corner shows the location of the bivariate mean for each feeding style. Each of the 220 species in the dataset is represented by 100 superimposed, translucent points, each point based on a distinct, alternative phylogeny, with species means shown as filled points. The SMA relations between bill length and hallux claw for the 100 phylogenies are plotted as superimposed bright green lines.

[Figure 5 near here]

The horizontal and vertical red lines in Fig. 5 represent median values for hallux claw (X) and exposed culmen (Y), separating the plot into quadrants. Counts of the number of each species, scored for each feeding style in each quadrant of Fig. 5, reveal—even more clearly than the slope of the SMA line—the functional link between large feet, short bills, and clinging to feed from flowers. The first four feeding styles in the legend of Fig. 5 (green, yellow, orange, and red dots), plus *Eutoxeres* (purple), all require clinging to feed. Of the 66 species known to

use these feeding styles, 31 lie in the lower-right quadrant (large feet, short bill), whereas only 16 or 17 would be expected by chance (Cohen's $W = 0.510$, a large effect size [Cohen 2013]; $P = 0.0007$ for chi-squared goodness-of-fit to equal representation in the 4 quadrants, with 11, 13, 11, and 31 species observed).

In contrast with clingers, the feeding style “feeds on the wing, through pierces” (10 species, blue dots in Fig. 5) had its mean (blue cross) and 5 of the 10 species in the lower left quadrant (short hallux claw, short bill), as might be expected for species that feed illegitimately to exploit flowers too long for their bill, but do so on the wing, and thus do not use their feet to cling (Fig. 1, photograph g) (Cohen's $W = 0.825$, a large effect size; sample size too small to compute chi-squared). The 144 species presumed (in the absence of any evidence to the contrary) to feed only legitimately, on the wing (black dots and black cross), were not significantly concentrated in any quadrant.

Assessing the roles of body mass, phylogeny, elevation, and sexual dimorphism. From the univariate analysis (Table S3), we know that clingers have shorter bills and longer hallux claws than non-clingers. The bivariate analysis revealed that these differences not only drive a negative correlation between bill and hallux claw for all species considered together (Figs. 4A and 5)—as might be expected—but also an even stronger negative correlation within clingers (Fig. 4B). The data for those analyses were filtered statistically to remove the influences of body mass, phylogeny, and elevation (triple-filtered), and they were based on intersexual means. We now consider the direct influences of body size (allometry), phylogenetic signal (the role of the Coquette clade), elevation above sea level, and sexual dimorphism. We demonstrate the crucial role of PGLS filtering in Supplemental Text S5: *Bill length vs. hallux claw without filtering*.

Allometry of clingers versus non-clingers. Do clingers differ from non-clingers in the relations between body mass and the size of bill or feet? Figure 6 shows simple allometric plots of bill size, tarsus, hallux claw, and middle-toe claw (Y), versus body mass (X), for clingers and non-clingers, with only the effects of phylogenetic autocorrelation filtered out (phylo-filtered PGLS scores, Supplemental Spreadsheet S1). All four characters are one-dimensional, so the expected slope would be $1/3$ for isometry (dimensional similarity, the dash-dot green lines in Fig. 6; see Supplemental Text S6: *Hummingbird body size and allometry: An overview*). The 95% confidence intervals for the slopes of each of the four characters in Fig. 6 (both for clingers and non-clingers) exceed the slope for isometry—although just barely, for middle-toe claw—so all are positively allometric (Table S5).

Allometric slope does not differ significantly between clingers and non-clingers for any of the four characters (Fig. 6 and Table S5), nor does the elevation (height above the X -axis) of the SMA line differ significantly between clingers and non-clingers for any of the three foot-characters. For bill size (exposed culmen, Fig. 6A), however, the line for clingers lies significantly ($P = 0.0002$) below the line for non-clingers: for a given body size, clingers have shorter bills, but do not differ significantly in hallux claw length (Fig. 6C). How, then, can we explain the fact that clingers have larger hallux claws than non-clingers, for triple-filtered data (Table S3), yet all species follow a statistically indistinguishable allometric relation for hallux claw for phylo-filtered data (Fig. 6C and Table S5)? The explanation is that clingers are, on average, larger than non-clingers in phylo-filtered body size—the red points lie further to the right along the allometric relations than the black triangles in Fig. 6A (Table S7, Hedges' $g_p = 0.3900$, $P = 0.0092$), a finding we discuss later in an evolutionary context.

The impact of the Coquettes on the overall results. To assess the impact of the Coquette clade on our results for hummingbirds as a whole, we repeated univariate and bivariate analyses for bill and hallux claw for Coquettes, alone, and for non-Coquettes (all other clades, combined). Within each of these two data subsets, we compared clingers *vs.* non-clingers, for triple-filtered data. The univariate analyses (Table S8) largely confirmed the family-level univariate pattern for each subset: hallux claws were substantially longer for the 29 Coquette clingers than for the 12 Coquette non-clingers, judging by effect size, for this necessarily small sample (Hedges' $g_p = 0.7384$, $P = 0.0887$), and likewise for the 36 non-Coquette clingers *vs.* the 132 non-Coquette non-clingers (Hedges' $g_p = 0.5990$, $P = 0.0381$). For bill length, non-Coquette clingers had shorter bills than non-Coquette non-clingers (Hedges' $g_p = 0.4858$, $P = 0.0016$). Coquette clinger bills were, likewise, shorter than Coquette non-clinger bills, but the effect size for the difference was small (Hedges' $g_p = 0.2751$), and its confidence interval spanned zero.

The Coquettes, just among themselves, confirmed the bivariate pattern for all hummingbird species in the study (Table S9), with a negative correlation between bill length and hallux claw (with even larger effect sizes, for all Coquettes and for Coquette clingers, than for all hummingbird species). Slopes for bill length *vs.* hallux claw for pooled non-Coquette clades were also negative, but the confidence intervals for effect sizes (r) spanned zero, despite the strong univariate results. Thus, for the bivariate results, Coquettes show a stronger relation than non-Coquettes between bill length and hallux claw, and thus disproportionately drive the significance for all species in the study, considered together (Fig. 5). Overall, however, the results indicate that the inverse pattern between bill length and hallux claw is consistent throughout the hummingbird family.

Relation between clinging and elevation above sea level. For previous analyses (except for allometry), we treated elevation above sea level (for each species, Supplemental Spreadsheet S1) as a confounding factor and filtered it out statistically. As discussed earlier, however, clinging to feed has been suggested to offer a particular advantage at higher elevations, where the costs of hovering are exacerbated by lower air density, lower partial pressure of oxygen, and lower temperatures. When we compared the mean elevation above sea level of species known to be clingers (1904 m a.s.l.) with the mean elevation of species not known to cling (non-clingers; 1105 m a.s.l.), we found that clingers, indeed, emerged as residents of higher elevations (Hedges' $g_p = 0.8073$, $P = 0.002$; Table S10). Just as with the negative relation between bill length and hallux claw, this pattern is stronger in the Coquette clade, but not exclusive to it. Pooled, non-Coquette clingers are also residents of higher elevations (1543 m a.s.l.) than non-Coquette non-clingers (1064 m a.s.l.) (Hedges' $g_p = 0.5441$, $P = 0.019$; Table S10). Even within the Coquette clade, for which our parsimony analysis suggests clinging is basal (Figs. 3, S3, and S4), Coquette clingers ($n = 29$ species) live at higher elevations (2364 m asl) than Coquette non-clingers (1561 m asl; $n = 12$ species), judging by effect size, for this necessarily small sample (Hedges' $g_p = 0.6357$, $P = 0.0662$; Table S10).

Results for sexes separately. Univariate comparisons, bivariate relationships, and allometric analysis for females and males, separately, proved to be almost entirely concordant with the intersex results. For each sex, clingers have substantially shorter bills and longer hallux claws than non-clingers, but tarsi do not differ between clingers and non-clingers (Table S11), just as for the intersex data (Table S3). Bill length and hallux claw are negatively correlated for each sex separately, as they are for intersex data, but more strongly for females than males (Table

S12). Allometric slopes for both sexes are positively allometric and highly significant for all three characters; none includes isometry in its confidence interval (Table S13).

Discussion

We have demonstrated a pattern of negative covariation between bill length and hallux claw length among hummingbird species, once the confounding effects of body size, elevation above sea level, and the potentially correlation-inflating effects of shared phylogeny have been statistically neutralized (Figs. 4 and 5). By comparing the bill length, hallux claw length, and tarsus length of hummingbirds with different feeding styles, we showed that species that cling to feed from flowers have shorter bills and longer hallux claws than species only known to feed legitimately on the wing. Clingers and non-clingers do not differ in tarsus length (Table S3), however, contrary to predictions based on biomechanical principles.

We have interpreted this pattern as a functional one, conjecturing that hummingbird species with longer bills tend to be forced by plant morphology to hover while feeding. Species with shorter bills, in contrast, can feed legitimately from short-corolla flowers, or they can steal nectar by piercing the base of long-corolla flowers or by feeding through pre-existing apertures (Fig. 1). These feeding styles favor clinging postures that benefit from longer hallux claws and larger feet (Fig. S1)—feeding styles that do not require the substantial energetic expense of hovering to feed.

The hallux is the key structure of the avian foot that enables perching and—especially—clinging behavior. A longer hallux claw expands the foot for added support while clinging, by reducing horizontal (reaction) forces normal to the substrate that would tend to pull the foretoe claws (and the bird's body) off the substrate (Fig. S1). In addition, a longer hallux claw may enhance substrate piercing, gaining purchase on soft substrates such as floral structures (Fig. 1,

photographs *c*, *f*, and *h*) (Norberg 1986; Norberg 1979; Winkler and Bock 1976). The hummingbird hallux claw is, at least statistically, a valid proxy for hallux length, based on a strong relationship ($r = 0.748$ [95% CI, 0.67, 0.81]; $P < 0.001$) between hallux claw length and hallux (toe) length measured on a subset of the species in Supplemental Spreadsheet S1 ($N = 155$) from which both measurements were obtained (Yanega 2007) (Fig. S8). In Supplemental Text S1 (*Discussion: The functional morphology of clinging*) we discuss the evolution of tarsus length in relation to clinging, review suggestive evidence for muscle modifications that may be associated with clinging in hummingbirds, and consider possible additional roles of the hallux claw.

Our interpretation implies the coordinated evolution of bill and foot in response to selection for efficient feeding (Feinsinger and Colwell 1978; Yanega 2007). Alternatively, perhaps selection has acted independently on bill size and foot size. For example, Stiles (2008) suggested that the characteristics of flowers (especially Asteraceae, Fig. 1, photograph *d*) common at higher elevations may select for shorter bills, whereas physiological challenges to performance at higher altitudes, including lower oxygen partial pressure, lower air density, and colder ambient temperatures (Altshuler and Dudley 2006; Carpenter 1976), may independently favor perching or clinging to feeding substrate, particularly in certain clades of hummingbirds—especially the Coquettes (Fig. 3).

Is the negative correlation between bill length and hallux claw driven by short bills and long claws among the (mostly high-elevation) Coquette clingers, together with long bills and short claws among the non-Coquettes? This suggestion is countered in four ways by our results: (1) our comparisons between clingers and non-clingers for bill length and hallux claw are based on triple-filtered data, with the confounding effects of phylogeny, elevation, and body size

neutralized; (2) we found that clinging to feed has some two dozen, independent evolutionary origins (Figs. 3, S3, and S4), only one of which parsimoniously accounts for clinging in the Coquettes; (3) both Coquettes (as a group) and non-Coquette clades (as a group), share the same pattern of longer hallux claws among clingers, compared with non-clingers (Table S8); and (4) we found the very same pattern of negative correlation between bill length and hallux claw *within* the Coquettes, themselves (Table S9).

The highly conserved relationship between some morphological characters—such as the allometry between wing length and body mass in hummingbirds ($r = 0.806$, Table S6)—is tightly enforced by biomechanical constraints (Altshuler et al. 2004; Feinsinger et al. 1979; Skandalis et al. 2017). In contrast, other morphological characters and relations appear remarkably free to vary in response to adaptive circumstances (*e.g.*, Colwell 1989; Temeles and Kress 2003), while nonetheless displaying a mean tendency of allometry with body size. In this study, as evidence for evolutionary lability, bill length, tarsus, hallux claw, and middle-toe claw vary impressively around the SMA lines that best define their relationships to one another (Figs. 5 and S5 and Table S4) and to body size (Fig. 6 and Table S5).

But what about the scatter? As discussed in Supplemental Text S4 (*Methods: Measurement error*), in an allometric (*e.g.*, Fig. 6) or bivariate morphometric (*e.g.*, Fig. 5) plot, the scatter around the SMA line is a mixture of measurement error (the degree to which measured values vary from the true values of the variates) and what Warton et al. (2006), Fuller (2009) and others call “equation error”—where the *true* values of variates do not fall exactly along a straight line. Here, we prefer to view substantial excursions from the underlying, bivariate or allometric SMA (after accounting for measurement error), not as “error” at all, but potentially as adaptive variation among species. In the study of allometry and other

morphometric relations, measurement error is noise, but adaptive variation among species is evolutionary music.

The repeated, independent association of short bills, long hallux claws, and clinging to feed offers a compelling example of convergent evolution—the independent evolution of phenotypic similarity (Arendt and Reznick 2008; Blount et al. 2018; Losos 2011). In this case, the association of a discrete behavioral trait with inversely directed values of two continuous morphological characters offers “pattern-based” evidence for convergence into a particular region of trait space (Fig. 5) (Stayton 2015). The fact that some two dozen independent origins of this association are required to account for the 66 hummingbird species (out of 220) that express it offers unusually strong statistical evidence (Mahler et al. 2017; Stayton 2015) for evolutionary convergence. But this multiplicity also invites inquiry into alternative morphological paths from orthodox feeding to clinging, while raising questions about the evolutionary persistence of the clinging behavior and its enabling morphology.

In the context of a negative correlation between bill length and hallux claw, adaptive transitions in the phylogeny between orthodox feeding and clinging to feed (Figs. 3, S3, and S4) imply a shift towards a shorter bill, towards longer hallux claws, or both, compared with ancestral states (Table S3). Given the evidence for multiple, independent transitions, it seems entirely possible that different paths have been followed in different instances (Losos 2011). A close look at the plots of allometry of bill length and hallux claw length (Fig. 6, panels A and C) reveals that clingers (red points) lie both well above and well below the SMA line that describes their mean relationship and cover virtually the entire scope of hummingbird body size. For bill length, the allometric line for clingers lies significantly below the line for non-clingers (clingers of a given body size have shorter bills). In contrast, the allometric relations for clingers and non-

clingers do not differ significantly for hallux claw, even though clingers have longer hallux claws than non-clingers when body size is filtered out (Table S5). We resolved this paradox by showing that clingers, on average, have larger bodies than non-clingers (Table S7). Perhaps the focus of selection is on hallux claws, in relation to the characteristics of clinging sites and feeding opportunities, and larger bodies are simply a correlated genetic response, possibly permitted by greater energy efficiency through clinging. Or perhaps larger body size, with allometrically larger hallux claws, could be an exaptation for clinging to feed in some transitions, and selection for shorter bills, independent of body size, is an alternative path towards shorter bills and longer hallux claws. These speculations invite further analysis of the data we have gathered (Supplemental Spreadsheet S1).

With the striking exception of the (apparently) basal transition from orthodox feeding to clinging in the Coquettes, most (known) transitions to clinging in the phylogeny (Figs. 3, S3A, and S4) are at or near the tips of the tree, many subtending only a single species—a pattern that suggests a puzzling lack of diversification and evolutionary persistence of lineages bearing the trait. Perhaps, in a community context, the role of clingers is subject to some kind of negative frequency-dependent fitness (Mahler et al. 2017), through competition with orthodox feeders, limiting the prevalence of the trait and possibly suppressing long-term persistence and phylogenetic diversification. Community-based biogeographical studies (*e.g.*, Sonne et al. 2019; Weinstein and Graham 2017) might begin to address this conjecture.

Conclusions

Hovering flight is a phenomenally expensive way to move between food sources and to extract energy from them. Living on the edge, energetically, favors any morphological or behavioral variant that offers a marginal advantage, given the constraints of the hummingbird body plan.

Most plant species with long-corolla flowers force long-billed species to forfeit the energetic advantage of clinging or perching to feed, offering no advantage to biomechanically enhanced feet, but generally offering large energetic rewards per flower. Short-billed hummingbirds are unsuited for legitimate feeding on long-corolla flowers, but they can reduce the high costs of hovering by clinging to feed legitimately on short-corolla flowers and to rob nectar from long-corolla flowers. By enhancing the grasp of the hummingbird foot, longer hallux claws and hallux toes are the key morphological features that enable the unorthodox tactic of clinging to feed. The repeated, independent evolution of these features in association with clinging to feed offers a compelling example of convergent evolution.

Acknowledgements

To the many collectors and preparators whose painstaking work made this study possible, and to the hummingbirds whose lives were sacrificed to provide a permanent and boundless source of information as museum specimens, we are most grateful. The following museums provided access to specimens: California Academy of Sciences (CAS), Cornell University Museum of Vertebrates (CUMV), Field Museum of Natural History (FMNH), Louisiana State University Museum of Zoology (LSUMZ), U.C. Berkeley Museum of Vertebrate Zoology (MVZ), Royal Ontario Museum (ROM), University of Connecticut Biodiversity Research Collections (UCONN), and the Yale Peabody Museum (YPM). For their advice and assistance with this 50-year project, we thank Robert Bleiweiss, Manfred Boehm, F. Lynn Carpenter, Agnes Dellinger, Peter Feinsinger, Jon Fjeldså, Douglas J. Futuyma, Johan Ingels, Frances C. James, Lou Jost, Margaret Lentell, Carlos Martínez del Río, Richard S. Miller, Shahid Naeem, Juan Francisco Ornelas, Fernando Ortiz-Crespo, Carsten Rahbek, J. V. Remsen, Margaret Rubega, Peter Scott, Jesper Sonne, Robert R. Sokal, F. Gary Stiles, Esther Quesada Tyrell, Peter C. Wainwright,

David B. Wake, David I. Warton, Larry L. Wolf, Richard Zusi, and the photographers acknowledged in the caption of Fig. 1. Reviewers and editors challenged us to further validate our results. Phylogenetic analyses were carried out by KF at the Computational Biology Core Facility of the University of Connecticut. AR-G is supported by the Walt Halperin Endowed Professorship and the Washington Research Foundation as Distinguished Investigator. TFR was supported by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, Brazil) and RKC and TFR by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES, Brazil). We dedicate this paper to the memory of Lynn Carpenter (1944-2022), whose pioneering work with high Andean hummingbirds inspired this project, 50 years ago.

Statement of Authorship

RKC conceived the study and planned the article, with substantial contributions from all other authors. RKC, GMY, and AR-G gathered the morphological data. KF did the phylogenetic analyses and prepared Figs. 3, S3, and S4. AR-G refined the systematics and nomenclature. TFR coded and performed the PGLS analyses and prepared the image in Fig. 5. DS prepared Fig. S1 and drafted the passages on functional morphology and biomechanics, with the assistance of AR-G and GMY. RKC drafted the rest of the article, carried out all other statistical analyses and prepared all other figures and tables. All authors contributed critically to revising the text and approved the final version.

Data and Code Availability

Data and code are available from the Harvard Dataverse repository:

<https://doi.org/10.7910/DVN/THDJCI> (Colwell et al. 2023).

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FIGURE CAPTIONS

Figure 1: Diagrammatic synopsis of the study (*left panel*) and examples of hummingbird feeding styles (*photographs on the right*). *Photographs a and b*: Feeding on the wing, legitimately (through the corolla mouth), by (*a*) a long-billed hummingbird on a long-corolla flower and (*b*) a short-billed hummingbird on a short-corolla flower. *Photographs c and d*: Short-billed hummingbirds feeding legitimately, while clinging. *Photograph e*: Feeding from the ground. *Photograph f*: A short-billed hummingbird (same species as in *b*) piercing a long-corolla flower to feed, while clinging (nectar robbery). *Photograph g*: A short-billed hummingbird piercing a long-corolla flower to feed, while hovering (nectar robbery). *Photograph h*: The unique case of *Eutoxeres* spp., with a long bill that is curved enough to allow clinging while feeding legitimately. All feeding styles besides feeding on the wing, legitimately (*a*), are designated as *unorthodox* in this study.

Species in the photographs (with bill lengths and photo credits): (*a*) *Phaethornis guy* (green hermit; bill length 39 mm) feeding on *Centropogon* sp. (Christian Sánchez Arce). (*b*) *Panterpe insignis* (fiery-throated hummingbird; bill length 19 mm) feeding on *Cavendishia* sp. (Christopher Becerra). (*c*) *Oreonympha nobilis* (bearded mountaineer; bill length 25 mm) feeding on *Nicotiana* sp. (Walter Mancilla Huaman). (*d*) *Oxypogon guerinii* (bearded

helmetcrest; bill length 8 mm) using its tail for support while clinging to feed on *Monticalia* sp. (János Oláh). (e) *Chalcostigma stanleyi* (blue-manteled thornbill; bill length 10 mm), feeding on *Gaultheria* sp. (Hal and Kirsten Snyder). (f) *Panterpe insignis* (fiery-throated hummingbird; bill length 19 mm) feeding on *Fuchsia* sp. (Christopher Becerra). (g) *Eupherusa eximia* (stripe-tailed hummingbird; bill length 18 mm) feeding on *Poikilacanthus* sp. (Michael and Patricia Fogden). (h) *Eutoxeres aquila* (white-tipped sicklebill; bill length 27 mm) clinging to *Heliconia* sp. flowers, about to feed from the uppermost flower (Roger Ahlman). Bill measurements from Supplemental Spreadsheet S1. All photographs used with permission.

Figure 2: Hummingbird morphological measurements. Measurements were recorded from museum specimens or living birds for tarsometatarsus (tarsus) (length), hallux toe (length), hallux claw (chord), middle-toe claw (chord), and wing length (chord) (Baldwin et al. 1931). Body mass (live weight in grams) is mostly from the literature but recorded from museum specimen tags or weights from field captures when necessary.

Figure 3: Phylogenetic origins of clinging to feed in hummingbirds. Points of origin were inferred using parsimony on a simplified consensus Bayesian topology with the manual addition of twelve taxa for which molecular data were not available (Table S1). Several non-clinging clades of hermits, bees, and emeralds were collapsed to simplify the figure. (Fig. S3A shows all 220 species.) Black branches represent non-clinging taxa; yellow branches indicate clinging taxa. On branches of the phylogeny for which parsimony inferred a 50% chance of clinging (indicated by a thin yellow stripe throughout the branch), a common origin was assumed, to estimate the number of independent origins of clinging conservatively. Each putative independent origin of clinging is marked with a yellow asterisk. Colored symbols at branch tips indicate specific feeding styles for individual taxa (as detailed in Supplemental Spreadsheet S1). See Fig . S3 for

additional inference about the phylogenetic origins of clinging. Hummingbird illustrations (Schuchmann 1999) by Hilary Burn, Jan Wilczur, Richard Allen, Norman Arlott, and H. Douglas Pratt.

Figure 4: Bivariate relationships (with SMA slopes—the number by each line) between bill length and foot-variables (tarsus, hallux claw, and middle-toe claw—MTC) for (A) all species, (B) clingers, and (C) non-clingers for triple-filtered data, intersexual means, adjusted for measurement error. Green lines show negative SMA slopes, and line thickness indicates the effect size for each slope: medium ($0.3 \leq r < 0.5$); small ($0.1 \leq r < 0.3$); none detected ($r < 0.1$) (Cohen 1992). Slopes for which the 95% confidence interval of effect size r spans zero are conservatively designated "no detectable effect," regardless of effect size r . See Table S4 for r , P , FDR , and other statistical details.

Figure 5: The relationship between bill length and hallux claw length for 220 hummingbird species, after filtering out the confounding effects of phylogenetic autocorrelation, body size, and elevation above sea level (triple-filtered data). Feeding style for each species is color-coded, as detailed in the inset legend (*upper right*). Each of the 220 species in the dataset is represented by 100 superimposed, translucent points, each point based on a distinct, alternative phylogeny. (A few individual points lie outside the graph.) Filled points are species means, and filled crosses are bivariate means for feeding styles, among the 100 phylogenies, as summarized in the callout (*lower left*). Red lines indicate median values for X and Y . For each of the 100 phylogenies, a diagonal bright green line shows the SMA relation between bill length and hallux claw length. The SMA relation for all species means yields effect size (correlation coefficient) $r = -0.1922$ [$-0.316 - 0.062$]; $P \leq 0.004$ (Table S4). Fig S6 shows the same data, but without graphical depiction of variation that arises from phylogenetic uncertainty.

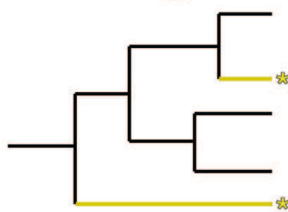
Figure 6: Allometric relationships between bill and foot characters and body size for clinger species (red points and red SMA lines) and non-clinger species (black triangles and black dashed SMA lines), after filtering out the effect of phylogenetic autocorrelation, taking measurement error (Table S2) into account for all variables. The dot-dash green line represents isometry (slope = 1/3). Each point represents the bivariate mean values (X and Y) of PGLS scores for a single species, averaged over 100 alternative phylogenies. All plotted allometric slopes have an effect size r (the product-moment correlation coefficient) of at least 0.2 (small)—although most are medium ($r = 0.3$) or large ($r = 0.5$) (Cohen 1992)—and the 95% confidence interval for r does not span zero, regardless of effect size. (By NHST criteria, each of the plotted relations satisfies $P < 0.02$ and $FDR < 0.03$.) See Table S5 for SMA slopes, SMA elevations (height above the X-axis), and statistical details. Table S6 gives the corresponding OLS slopes and intercepts, although we do not endorse OLS for allometry (see Supplemental Text S6: *Statistics of allometry*).

Figure 1

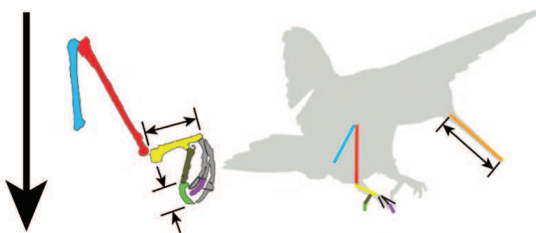
Scoring species by feeding style



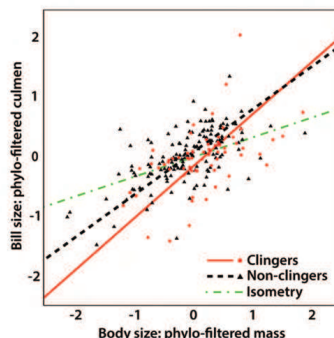
Phylogenetic origins of clinging



Measuring specimens



Analysis



Interpretation

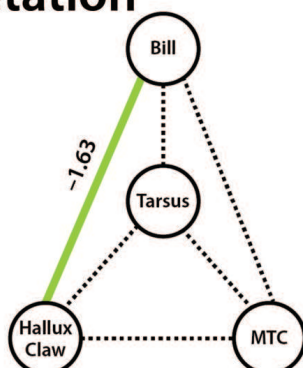


Figure 2

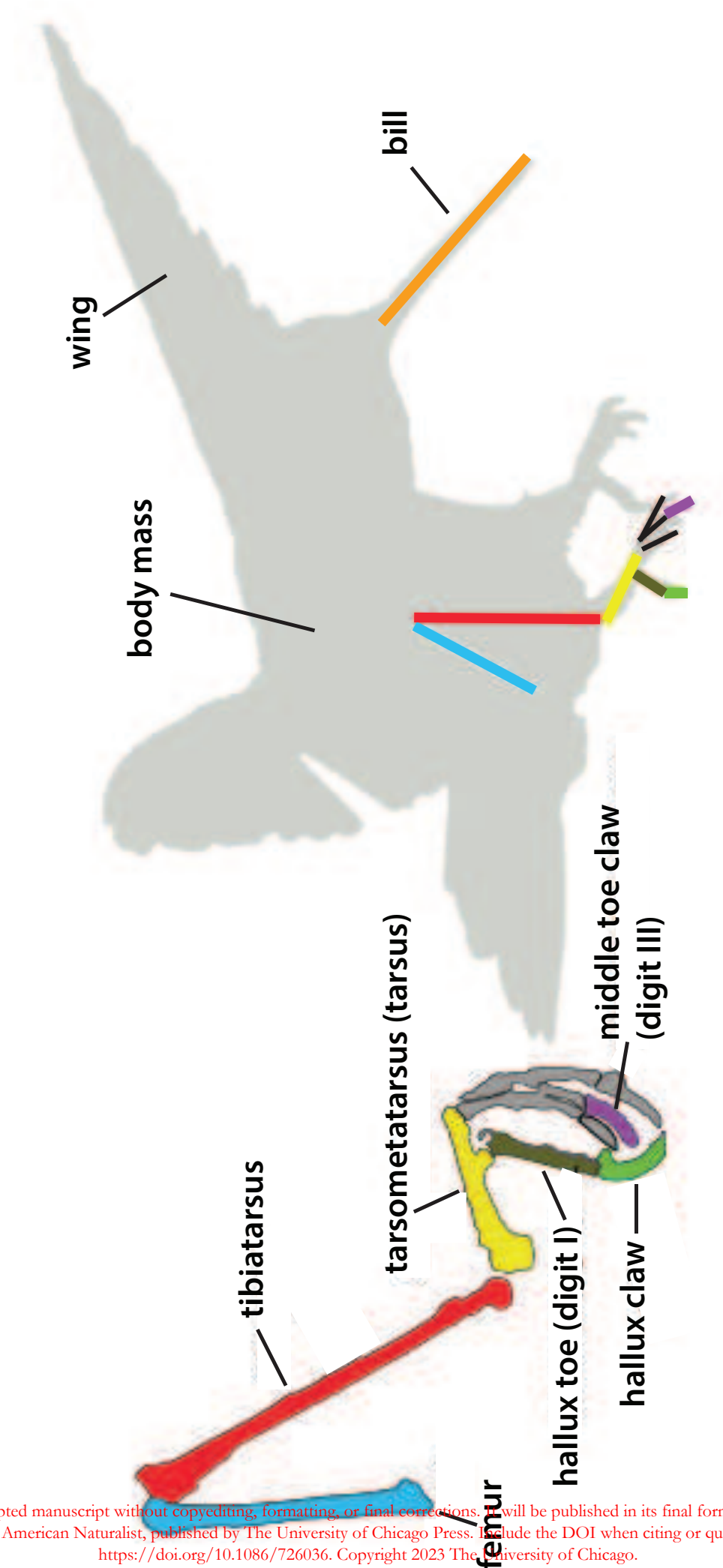
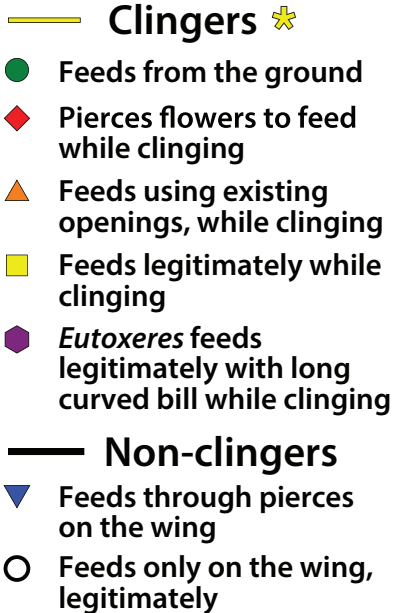


Figure 3



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Figure 4

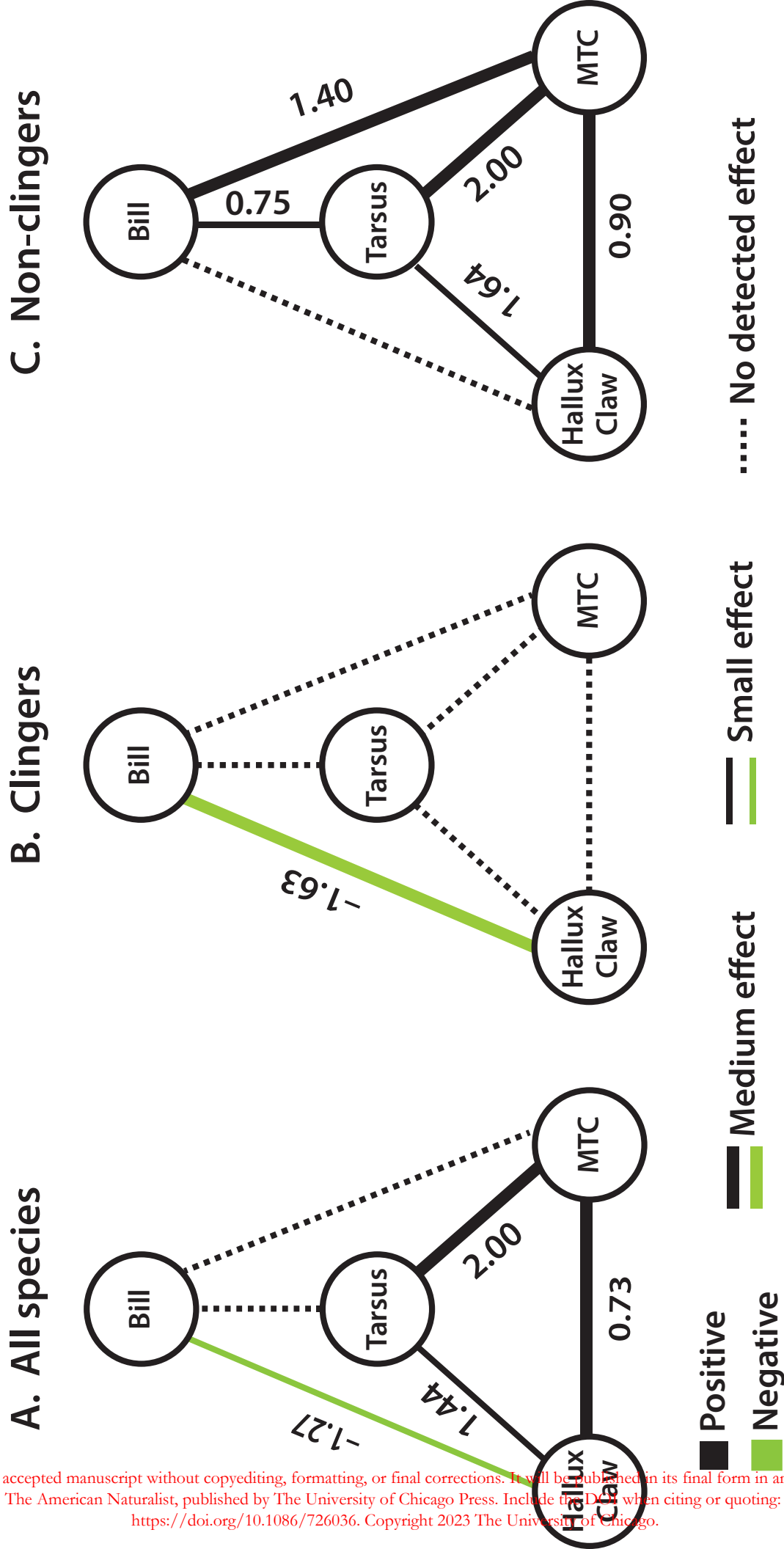


Figure 5

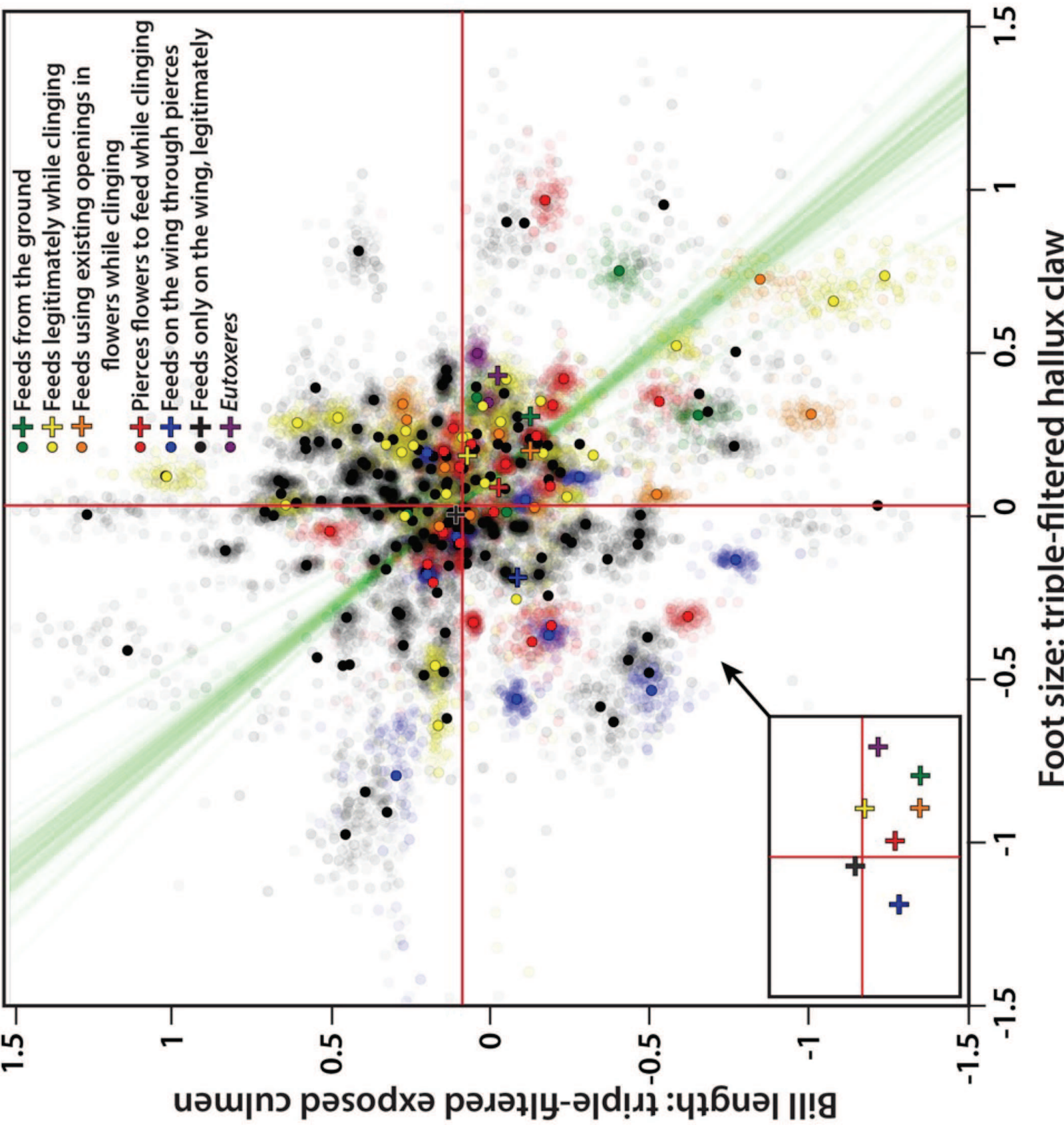
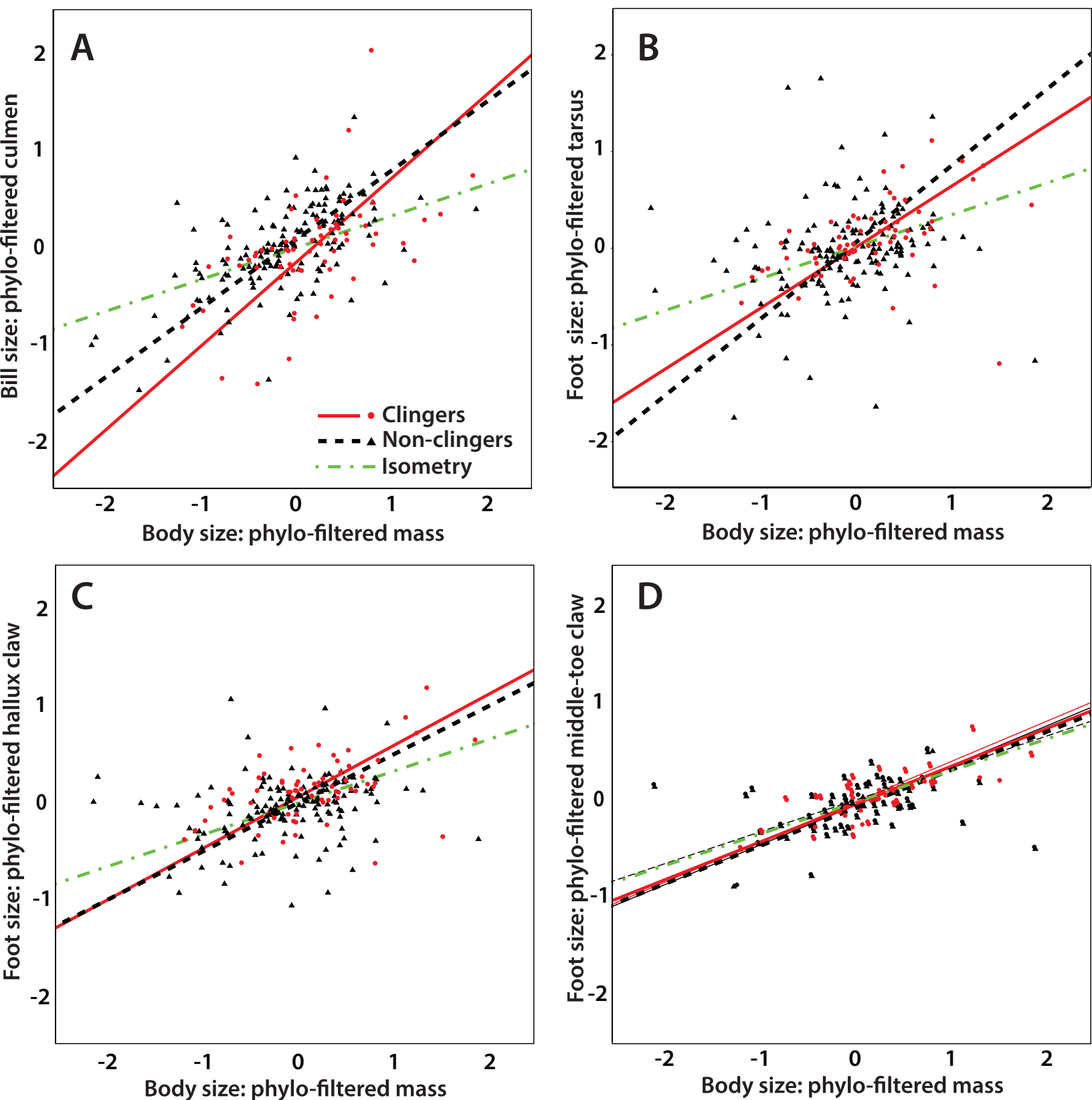


Figure 6



Online Supplement for:

Repeated Evolution of Unorthodox Feeding Styles Drives a Negative Correlation Between Foot Size and Bill Length in Hummingbirds

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Supplemental Figures S1–S8

Supplemental Tables S1–S14

Supplemental Text S1–S7

Supplemental Figures

Figure S1: The mechanics of clinging in hummingbirds.

Figure S2: Feeding style assignment strategy and the number of species in each category.

Figure S3A: Phylogenetic origins of clinging, showing all 220 species in the study.

Figure S3B: Phylogeny and the origins of clinging: sensitivity analysis.

Figure S4: Phylogeny and the origins of clinging: model-based ancestral state reconstruction of feeding styles.

Figure S5: Bivariate relationships between bill and foot characters for clinger species and non-clinger species.

Figure S6: The relationship between bill length and hallux claw length, showing mean values only (same data as Fig. 5, but without phylogenetic uncertainty).

Figure S7: Raw (unfiltered) log bill length vs. raw log hallux claw chord.

Figure S8: SMA relation between the chord of the hallux claw and length of the hallux toe (not including the claw).

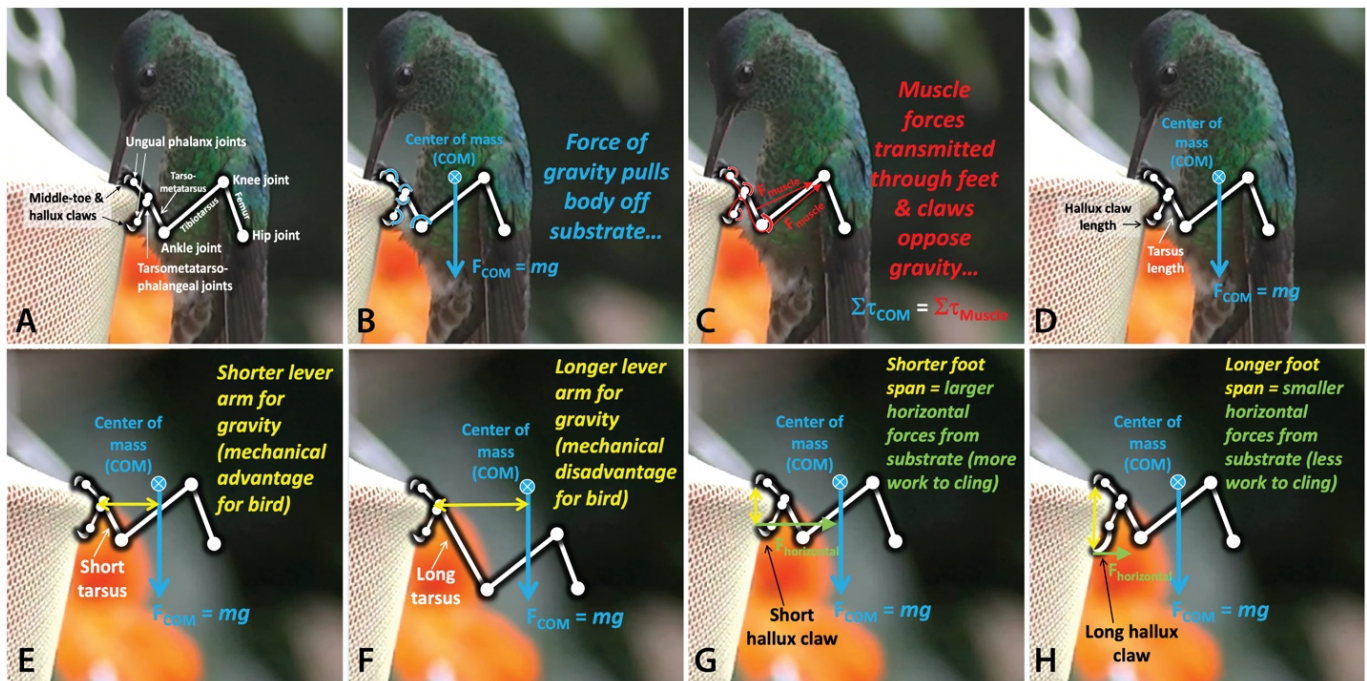


Figure S1: The mechanics of clinging in hummingbirds. **A.** Anatomy of the leg in a clinging hummingbird. **B., C., and D.** Balance of forces affecting clinging ability (adapted from Norberg [1979]). **E. and F.** The mechanical advantage a shorter vs. a longer tarsus. **G. and H.** The mechanical advantage a longer vs. a shorter hallux claw. Image of *Amazilia cyanifrons* (indigo-capped hummingbird), clinging to an artificial feeder, from a video by A.R.-G. Drawings and text by D.S.

	Feeds from the ground	Feeds legitimately while clinging	Feeds using existing openings in flowers, while clinging	Pierces flowers to feed while clinging	Feeds through pierces on the wing	Feeds only on the wing, legitimately
Feeds from the ground	6	←				
Feeds legitimately while clinging		28				
Feeds using existing openings in flowers, while clinging		→	11			
Pierces flowers to feed while clinging		→	→	21		
Feeds through pierces on the wing					10	
Feeds only on the wing, legitimately						144

Figure S2: Feeding style assignment strategy and the number of species in each category. To simplify the classification for analysis, if a species was scored for more than one feeding category, we assigned it to the most “derived” feeding style it is known to adopt. Arrows indicate category assignment for species with multiple unorthodox feeding strategies. For example, a species that feeds legitimately while clinging (yellow) and also feeds using existing openings while clinging (orange) would be assigned to the latter (more “derived”) category. However, as far as we can ascertain, all unorthodox feeders also feed on the wing, legitimately.

Figure S3A: [Previous page.] Phylogenetic origins of clinging to feed in hummingbirds, showing all 220 species in the study. (This figure is otherwise identical to Main Text Fig. 3, which omits several non-clinging clades of hermits, bees, and emeralds to simplify the figure.) Points of origin were inferred using parsimony on a simplified consensus Bayesian topology with the manual addition of twelve taxa for which molecular data were not available (Table S1). Black branches represent non-clinging taxa; yellow branches indicate clinging taxa. On branches of the phylogeny for which parsimony inferred a 50% chance of clinging (indicated by a thin yellow stripe throughout the branch), a common origin was assumed, to estimate the number of independent origins of clinging conservatively. Each putative independent origin of clinging is marked with a yellow asterisk. Colored symbols at branch tips indicate specific feeding styles for individual taxa (as detailed in Supplemental Spreadsheet S1). Hummingbird illustrations (Schuchmann 1999) by Hilary Burn, Jan Wilczur, Richard Allen, Norman Arlott, and H. Douglas Pratt.

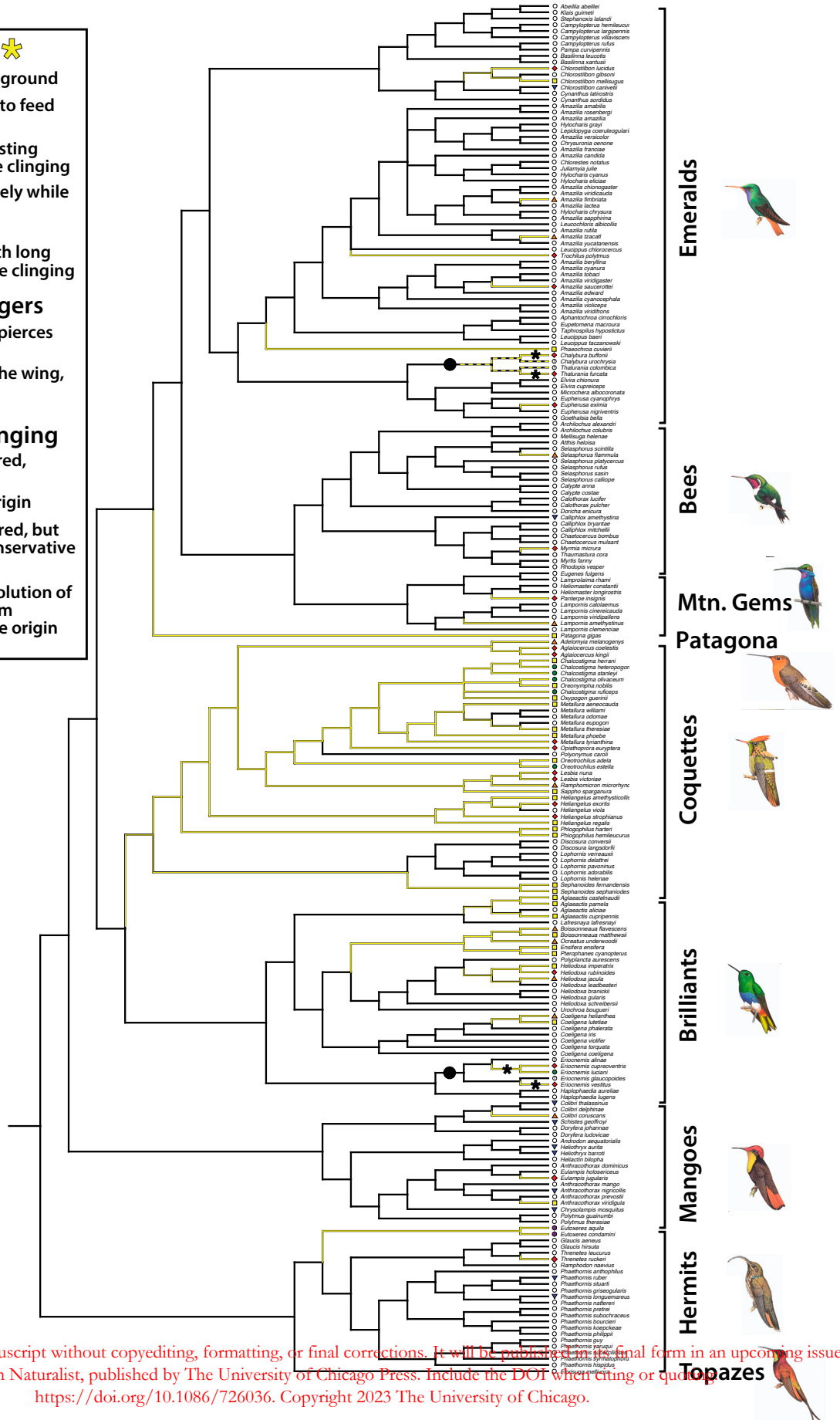
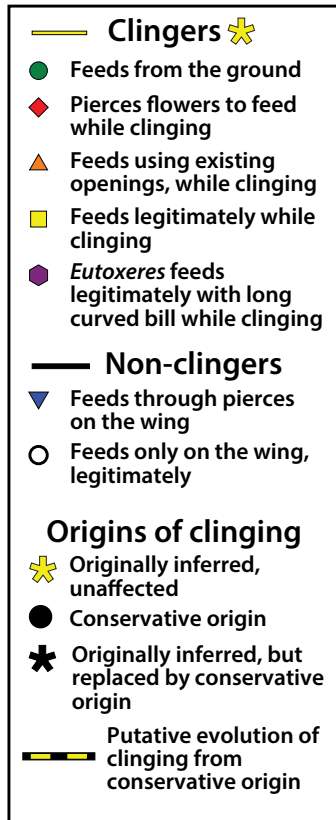


Figure S3B: [Previous page.] Phylogeny and the origins of clinging: sensitivity analysis.

Character mapping modified from Main Text Fig. 3 and Fig. S3A, so that any two instances of clinger origination separated by only one subtending node are assumed to have clingers as their most recent common ancestor, thus designating a single origin of clinging behavior for both species (or clades) of each such pair. The solitary long branch of the morphologically unique species *Patagona gigas* (Groom et al. 2018; Shankar et al. 2020) was not considered for this modified inference. This exercise had virtually no effect, reducing the initial 26 only to 24 independent origins. Every named clade of hummingbirds (with the exception of the small—four-species—Topaz clade, with only one species on our reconstructed phylogeny) nonetheless had one or more independent origins of clinging.

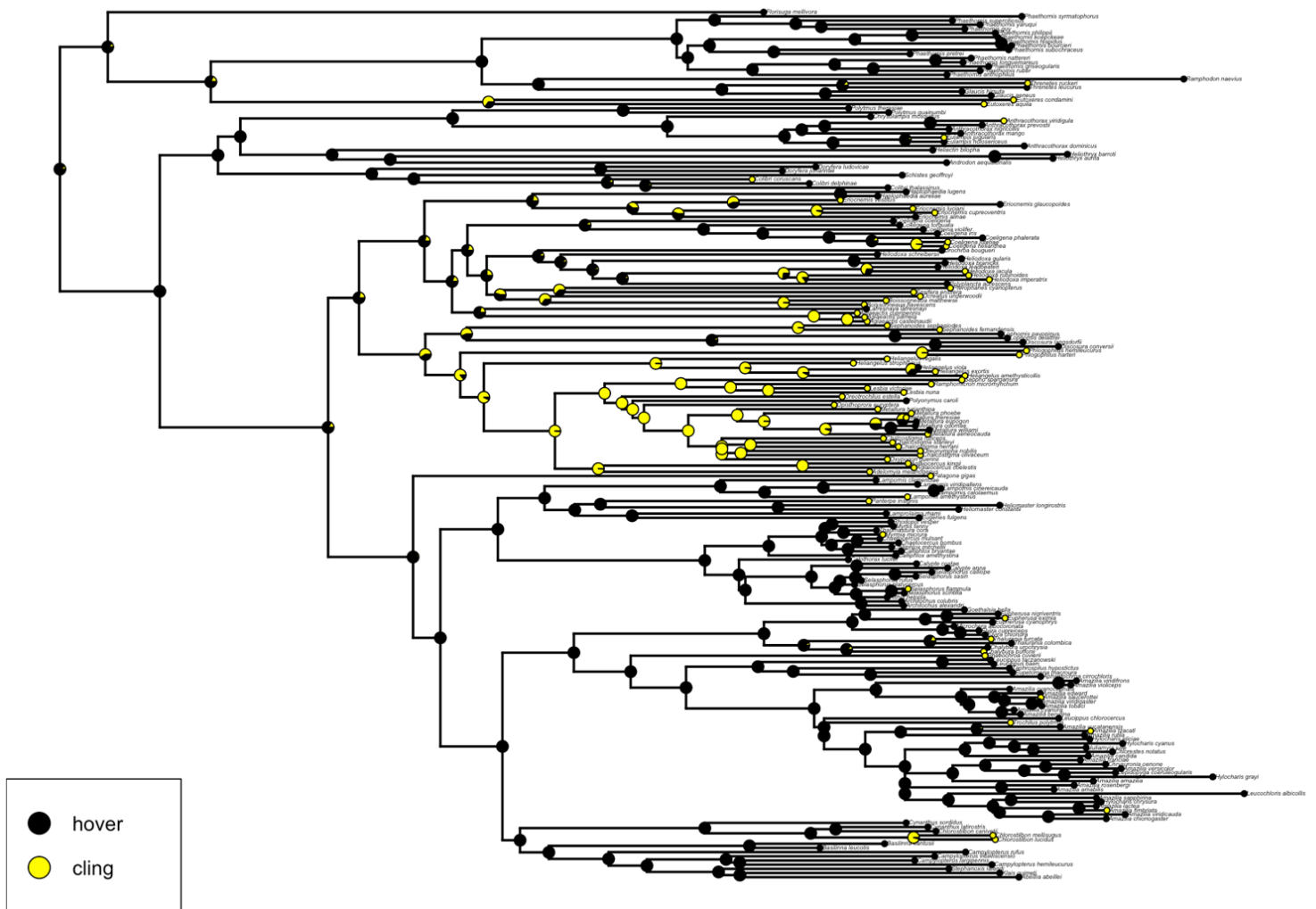


Figure S4: Phylogeny and the origins of clinging: model-based ancestral state reconstruction of feeding style in hummingbirds. Feeding styles were mapped onto a Bayesian consensus phylogeny (based on the data of McGuire et al. [2014]) using the ER model with 100 simulations (Revell 2012). In the simulation results, to determine the number of character state changes in the tree, a node with more than 50% black was considered an ancestor that exclusively hovered to feed, a node with more than 50% yellow a clinger ancestor. Pie charts at nodes represent the odds of the ancestor being a hoverer or clinger. *Black*: hovering only; *yellow*: clinging to feed in addition to hovering. The tree shows a total of 27 putative origins of clinging, all but one of which is supported by our parsimony analysis (Figs. 3 and S3) as well.

In the Hermit clade, clinging originated twice: once in the ancestor of *Threnetes ruckeri* and once in the ancestor of the genus *Eutoxeres*. Among Mangoes, there are three origins: *Anthracocorax viridigula*, *Eulampis jugularis*, and *Colibri coruscans*. *Patagona* represents another origin. Mountain Gems contain two additional origins in *Lampornis amethystinus* and *Panterpe insignis*, and Bees two more: *Myrmia micrura* and *Selasphorus flammula*. In Emeralds, nine transitions from orthodox feeding to clinging are indicated: *Chlorostilbon*, *Amazilia fimbriata*, *A. saucerottei*, *A. tzacatl*, *Trochilus polytmus*, *Phaeochroa cuvierii*, *Chalybura buffoni*, *Thalurania furcata*, and *Eupherusa eximia*.

The parsimony analysis and the model-based ancestral state reconstruction also agree that clinging is ancestral to Coquettes. The parsimony reconstruction (Figs. 3 and S3) infers six origins of clinging within Brilliants (*Eriocnemis vestitus*; *E. cupreovertris* + *E. luciani*; *Coeligena lutetiae* + *C. helianthea*; *Heliodoxa imperatrix* + *H. rubinoides* + *H. jacula* (a putative reversal in *H. leadbeateri*); *Boissonneaua flavescens* + *B. matthewsii* + *Ocreatus underwoodii* + *Ensifera ensifera* + *Pterophanes cyanopterus*; and *Aglaeactis*), whereas the model-based reconstruction shows an additional state switch: instead of a single origin of clinging in the *Boissonneaua/Ensifera* clade, the ancestor of *Boissonneaua* and *Ocreatus* represent one origin and the ancestor of *Ensifera* represent another origin.

The R code for this analysis is available at [DOI: 10.5281/zenodo.7618899](https://doi.org/10.5281/zenodo.7618899)

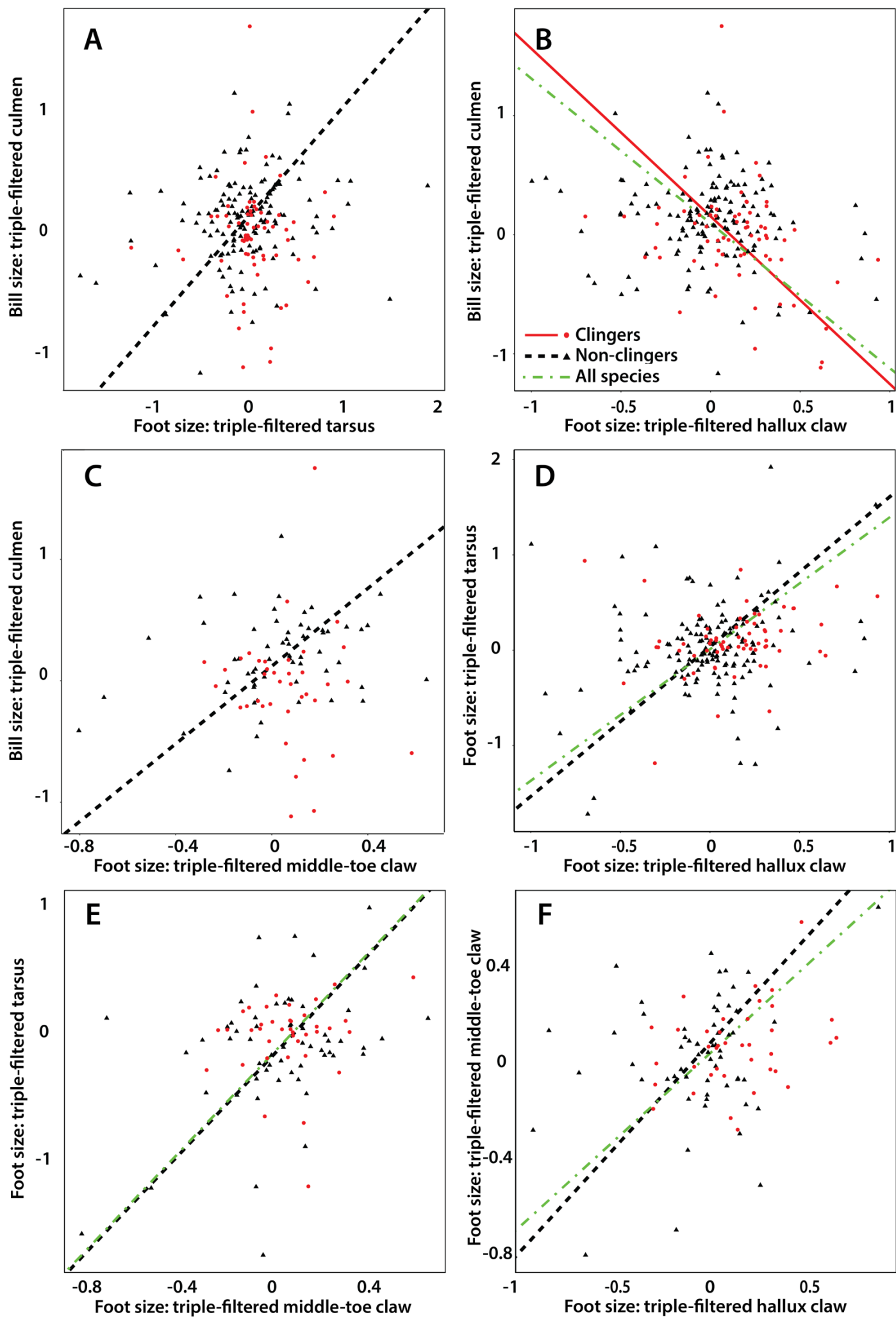


Figure S5: [Previous page.] Bivariate relationships between bill and foot characters for clinger species (red points) and non-clinger species (black triangles), after filtering out the confounding effects of phylogeny, body size, and elevation above sea level (triple-filtered data), taking measurement error (Table S2) into account for all variables. Fitted SMA lines are shown only for bivariate relations for which effect size r (the product-moment correlation coefficient) is at least $|0.1|$ —a "small" effect size (Cohen 1992a)—and the 95% confidence interval for r does not span zero, regardless of effect size. A red line indicates a bivariate relation that meets these criteria for clingers, a dashed black line for non-clingers, and a dot-dashed green line for all species pooled. Each point represents the bivariate mean values (X and Y) of PGLS scores for a single species, averaged over 100 alternative phylogenies. See Table S4 for SMA slopes, SMA elevations, r , P , FDR , and other statistical details.

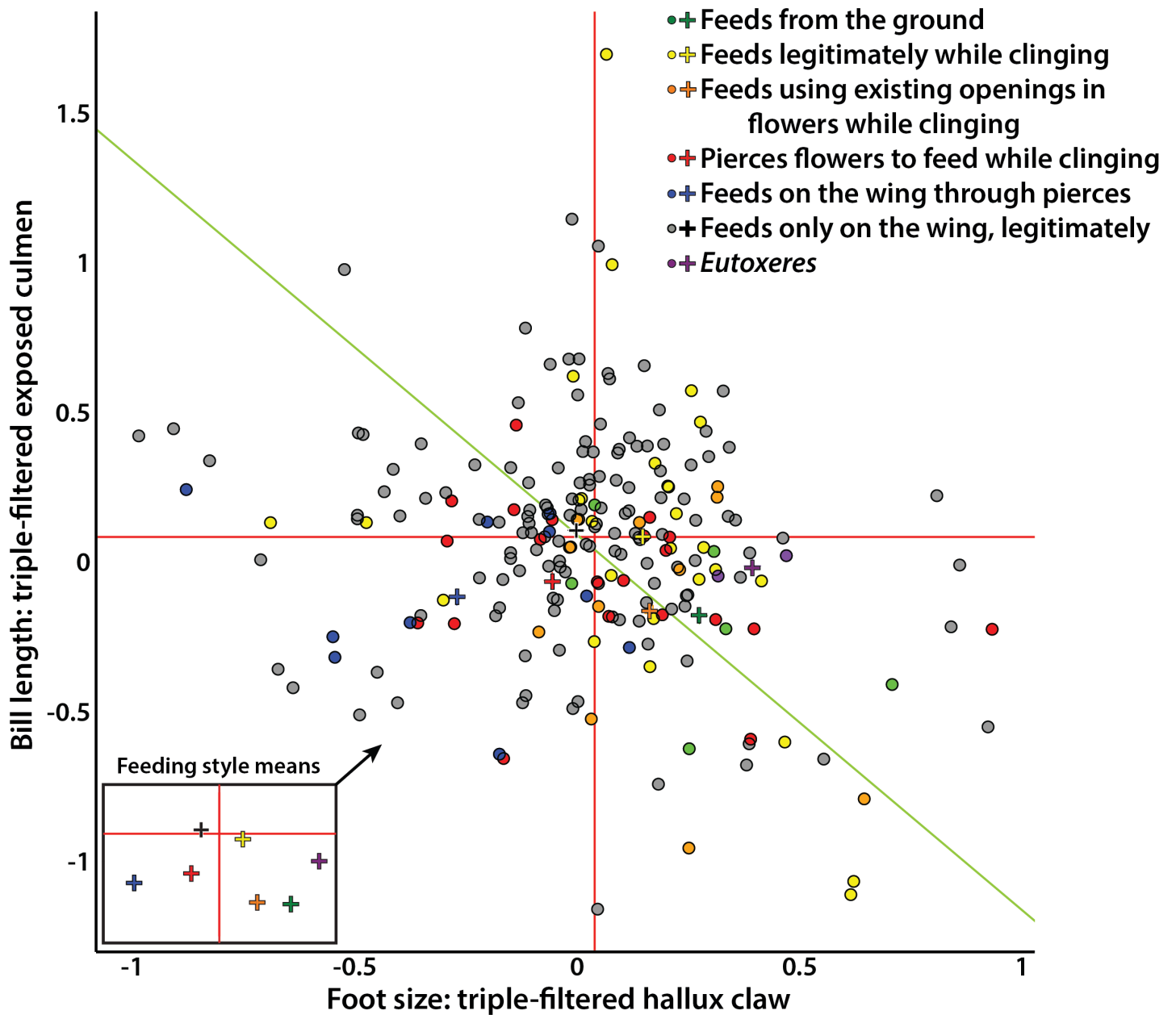


Figure S6: The relationship between bill length and hallux claw length, showing mean values only, in relation to feeding styles. (The figure is based on exactly the same data as Main Text Fig. 5, but without depicting phylogenetic uncertainty graphically). See the caption of Fig. 5 for details.

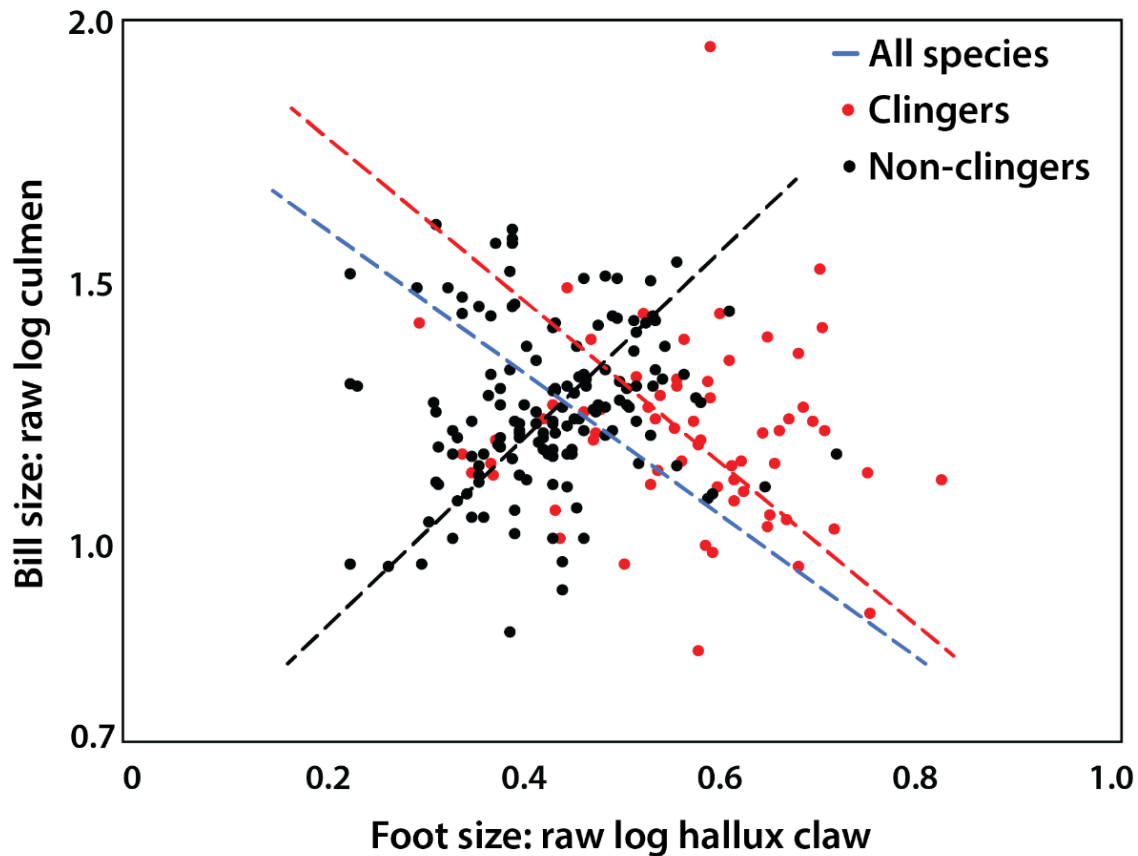


Figure S7: Raw (unfiltered) log bill length vs. raw log hallux claw chord. The confidence interval for effect size (r) for each of the three SMA lines (*blue*: all species; *red*: clingers; *black*: non-clingers) spans zero; $P \gg 0.05$ for each correlation. Logs to base 10. Details in Table S14.

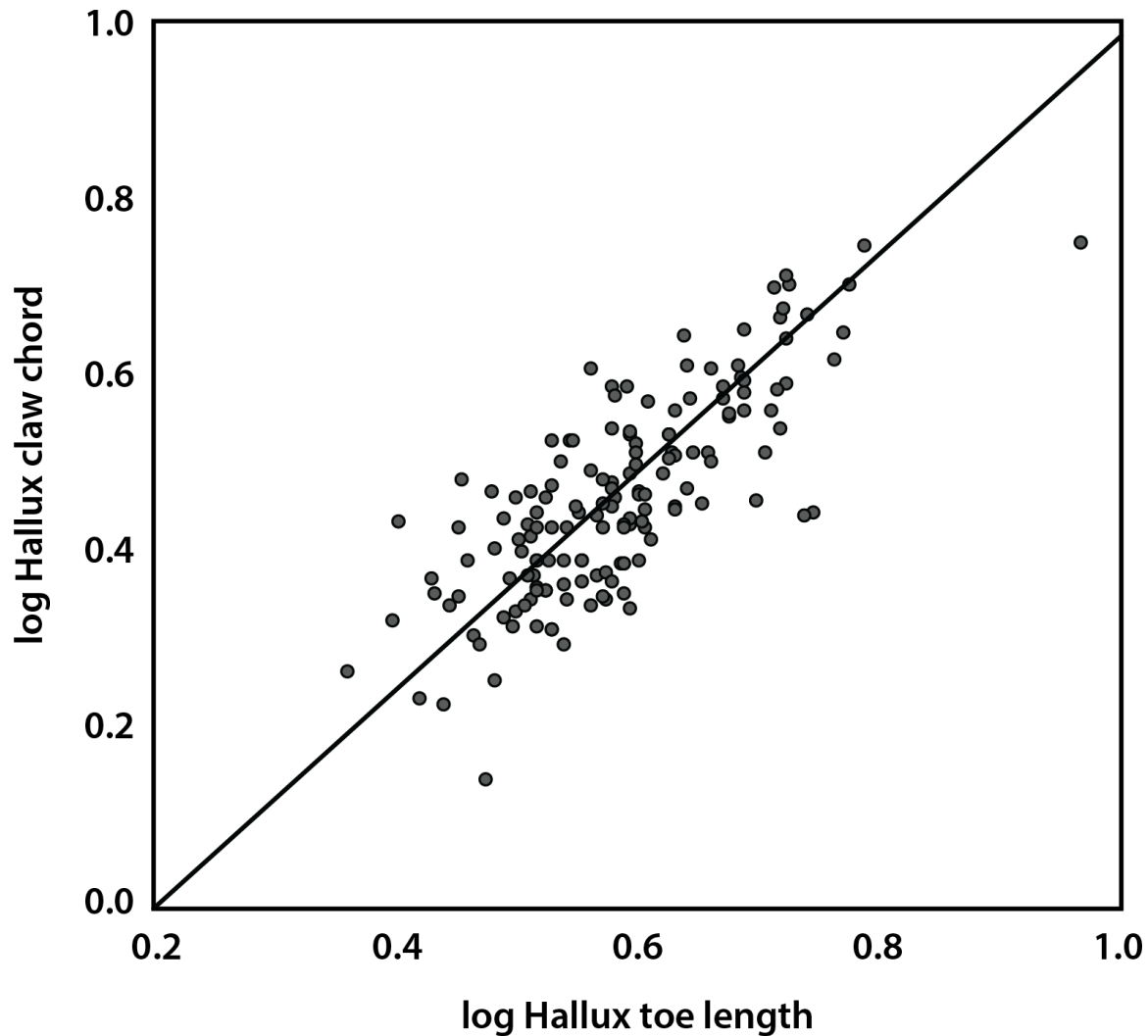


Figure S8: SMA relation between the chord of the hallux claw and length of the hallux toe (not including the claw), measured on a subset of the species in Supplemental Spreadsheet S1 ($N = 155$) from which both measurements were obtained (Yanega 2007). The close correspondence (SMA slope = 1.225 [95% CI, 1.109, 1.353], $r = 0.748$ [95% CI, 0.67, 0.81], $P < 2.22\text{e-}16$) shows that hallux claw length, by itself, serves as a reliable indicator of hallux toe length and of overall hallux size.

Supplemental Tables

Table S1: Phylogenetic placement of species not in the McGuire phylogeny.

Table S2: Measurement error variance, Pagel's lambda, and phylogenetic error variance.

Table S3: Univariate analysis on triple-filtered data.

Table S4: Bivariate SMA slopes and elevations between triple-filtered bill and foot characters.

Table S5: Bill, foot, and wing allometry, with confidence intervals, computed with SMA, based on phylogenetically filtered PGLS scores.

Table S6: Bill, foot, and wing allometry, with confidence intervals, computed with OLS, based on phylogenetically filtered PGLS scores.

Table S7: Univariate analysis of phylo-filtered body mass for clingers vs. non-clingers.

Table S8: Univariate analysis of triple-filtered data for the Coquette clade vs. pooled non-Coquette clades, comparing bill and foot elements for clingers vs. non-clingers.

Table S9: SMA slopes and elevations between bill length (exposed culmen) and hallux claw, for the Coquette clade, pooled non-Coquette clades, and (from Table S4) all species.

Table S10: Mean elevation above sea level for clingers vs. non-clingers for all species, for the Coquette clade, and for pooled non-Coquette clades.

Table S11: Univariate analysis on triple-filtered data for males and females.

Table S12: Bivariate SMA slopes and elevations for males and females.

Table S13: Allometric slopes and elevations (SMA) for males, females, and (from Table S5) both sexes combined.

Table S14: SMA slopes and elevations between bill length and hallux claw, for raw data (log 10 transformed).

Table S1: Phylogenetic placement of species not in the McGuire phylogeny. Using the method of (Rangel et al. 2015), we placed these “phylogenetically uncertain taxa” (PUTs) in each of the 100 alternative phylogenies, at random, within the “most derived consensus clade” (MDCC) that unequivocally contains each PUT, without creating polytomies.

Species		PUT placement
1	<i>Aglaeactis aliciae</i>	Make sister of <i>A. cupripennis</i>
2	<i>Calothorax pulcher</i>	Make sister of <i>Calothorax lucifer</i>
3	<i>Calypte helenae</i>	Make sister of <i>Calliphlox evelynae</i> (now <i>Nesophlox evelynae</i>), and call it <i>Mellisuga helenae</i> (see paper from previous line)
4	<i>Campylopterus curvipennis</i>	Make sister of <i>Campylopterus excellens</i> (in the phylogeny), and call them <i>Pampa curvipennis</i> and <i>Pampa excellens</i>
5	<i>Chalcostigma heteropogon</i>	Make sister of <i>Chalcostigma herrani</i>
6	<i>Chlorostilbon gibsoni</i>	Make sister of <i>Chlorostilbon mellisugus</i>
7	<i>Doricha enicura</i>	Make sister of <i>Doricha eliza</i>
8	<i>Lophornis adorabilis</i>	PUT basal in genus (3 spp in phylogeny) as sister of <i>Lophornis helenae</i>
9	<i>Lophornis helenae</i>	PUT basal in genus (3 spp in phylogeny) as sister of <i>Lophornis adorabilis</i>
10	<i>Lophornis verreauxii</i>	Make sister of <i>Lophornis chalybeus</i>
11	<i>Oreotrochilus adela</i>	PUT basal in genus (4 spp in phylogeny)
12	<i>Phaethornis stuarti</i>	Make sister of <i>Phaethornis ruber</i>

Authorities

1	Zimmer (1951) suggested that <i>Aglaeactis aliciae</i> could be treated as a subspecies of <i>Aglaeactis cupripennis</i> ; Fjeldsø & Krabbe (1990) considered all the <i>Aglaeactis</i> to form a superspecies.
2	https://onlinelibrary.wiley.com/doi/10.1111/evo.13432
3	http://checklist.aou.org/nacc/proposals/comments/2019_D_comments_web.html
4	http://www.museum.lsu.edu/~Remsen/SACCprop780.htm

5	https://tinyurl.com/2p9dv6w3
6	https://www.researchgate.net/publication/321277435_The_generic_classification_of_the_Trochilini_Aves_Trochilidae_Reconciling_taxonomy_with_phylogeny
7	https://onlinelibrary.wiley.com/doi/10.1111/evo.13432
8	Del Hoyo et al. (2018).
9	Del Hoyo et al. (2018).
10	http://www.museum.lsu.edu/~Remsen/SACCprop833.htm
11	http://www.museum.lsu.edu/~Remsen/SACCprop808.htm
12	Peters (1945) questioned whether <i>Phaethornis stuarti</i> was a species or just a subspecies of <i>P. ruber</i> , but they are clearly separate species (e.g., Zimmer 1950a, Meyer de Schauensee 1970, Schuchmann 1999).

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- Del Hoyo, J., A. Elliott, J. Sargatal, D. Christie, and E. de Juana. 2018. *Handbook of the birds of the world alive*. Barcelona: Lynx Edicions.
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- Zimmer, J. T. 1950. *Studies of Peruvian birds*. No. 55, The hummingbird genera *Doryfera*, *Glaucis*, *Threnetes*, and *Phaethornis*. American Museum Novitates, no. 1449.
- Zimmer, J. T. 1951. *Studies of Peruvian birds*. No. 61. The genera *Aglaeactis*, *Lafresnaya*, *Pterophanes*, *Boissonneaua*, *Heliangelus*, *Eriocnemis*, *Haplophaedia*, *Ocreatus*, and *Lesbia*. American Museum Novitates, no. 1540, pp. 1-55.

Table S2: Measurement error variance, Pagel's lambda, and phylogenetic error variance.

Measurement error variance was estimated as the sample variance, among individuals, within species, of \ln -transformed measurements for each species in our dataset (Harvard Dataverse repository) for which we measured 2 or more individuals. (For key morphometric characters, the number of species with 2 or more individuals ranged from 182 to 203 species, depending on the character.) For each character, we combined these variances as a weighted average using Eq. 31 of Warton et al. (2006). For body mass, we used all available museum specimen tag weights and field weights from captured individuals (198 species, of which 162 had two or more individuals) from our original dataset. Because we measured middle-toe claw for only a single specimen of each of 103 species, measurement error could not be estimated for this trait. *Pagel's lambda* was computed for each character, with (*adjusted*) and without (*raw*) accounting for measurement error variance, using the R (R Core Team 2021) packages *geiger* (Harmon et al. 2008) and *phytools* (Revell 2012). *Phylogenetic error variance* was estimated as the weighted average of the sample variance, among 100 alternative phylogenies, within species, of triple-filtered PGLS residuals for each species in our dataset, using Eq. 31 of Warton et al. (2006).

Character	Body mass	Exposed culmen	Tarsus	Hallux claw	Middle-toe claw	Wing	Mean
Measurement error							
Mean of \ln measurements	1.5662	2.9508	1.7043	1.0662	0.0380	4.0194	
Total variance of \ln measurements	0.1641	0.1117	0.0418	0.0705	0.0480	0.0505	0.0811
N for total variance	198	220	218	220	103	198	
Measurement error variance	0.0060	0.0012	0.0049	0.0053		0.0009	0.0037
N for error variance	162	204	182	203		220	
Natural variance (total variance – measurement error variance)	0.1581	0.1165	0.0370	0.0652		0.0496	0.0853
Proportion measurement error variance	0.0367	0.0100	0.1161	0.0752		0.0184	0.0513
Pagel's lambda							
Pagel's lambda (raw)	0.9520	0.9880	0.7480	0.9190	0.9380	0.9370	0.9137
Pagel's lambda adjusted for measurement error variance	0.9730	0.9890	0.8310	0.9610		0.9530	0.9414
Phylogenetic error variance							
Mean of PGLS triple-filtered intersex scores		0.0738	0.0444	0.0315	0.0383		0.0470
N for phylogenetic variance		220	220	220	103		
Total variance of PGLS triple-filtered intersex scores		0.1500	0.1910	0.0949	0.0480		
Weighted mean phylogenetic error variance (variance of PGLS triple-filtered intersex scores) among species		0.000078	0.000244	0.000131	0.000024		0.000119
Proportion of total phylogenetic variance		0.000522	0.001276	0.001384	0.000506		0.000922

Hummingbird Foot Size and Bill Length, Online Supplement p. 20

Table S3: Univariate analysis on triple-filtered data. Bill and foot elements for clingers vs. non-clingers, with and without outliers. Outliers significant at $P < 0.05$ were determined by iterative Grubbs' test. Effect size is Hedges' g_p . Effect sizes (g_p): small 0.2, medium 0.5, large 0.8 (Cohen 1992a). P (equal variances) determined by F -test. P (equal means) determined by t -test (for unequal variances, if necessary). False discovery rate (FDR) computed for all P -values in this table, as a family of results. *Yellow highlight* indicates *higher value* for results with Effect Size (ES) > 0.3 and CI not spanning zero, and/or P or $FDR < 0.05$.

[The table appears on the next page.]

Hummingbird Foot Size and Bill Length, Online Supplement p. 21

Bill	Clingers				Non-clingers				Effect Size	NHST comparisons			
	N	Mean	SD	Outliers	N	Mean	SD	Outliers	Hedges' g_p [95% CI]	P (equal variance)	P (equal means)	FDR (equal variance)	FDR (equal means)
All species	66	-0.0161	0.4423	1	144	0.1279	0.3551	0	0.3681 [0.0755, 0.6625]	0.0174	0.0239	0.0406	0.0478
No outliers	65	-0.0413	0.3867	0	144	0.1274	0.3551	0	0.4617 [0.1666, 0.7591]	0.2319	0.0021	0.2706	0.0098
									Clinger bills shorter (and more variable, when the single outlier— <i>Ensifera</i> —is included)				
Tarsus	Clingers				Non-clingers				Effect Size	NHST comparisons			
	N	Mean	SD	Outliers	N	Mean	SD	Outliers	Hedges' g_p [95% CI]	P (equal variance)	P (equal means)	FDR (equal variance)	FDR (equal means)
All species	65	0.0951	0.3335	0	143	0.0246	0.4714	4	0.1622 [-0.1311, 0.4561]	0.0010	0.2194	0.0084	0.2706
No outliers	65	0.0951	0.3335	0	139	0.0241	0.3824	0	0.1924 [-0.1022, 0.4880]	0.2020	0.1004	0.2706	0.1757
									Clinger tarsus less variable (with outliers only)				
Hallux Claw	Clingers				Non-clingers				Effect Size	NHST comparisons			
	N	Mean	SD	Outliers	N	Mean	SD	Outliers	Hedges' g_p [95% CI]	P (equal variance)	P (equal means)	FDR (equal variance)	FDR (equal means)
All species	66	0.1383	0.2810	0	144	-0.0066	0.3049	0	0.4851 [0.1912, 0.7813]	0.2164	0.0012	0.2706	0.0084
									Clinger hallux claws longer.				
Middle-toe Claw	Clingers				Non-clingers				Effect Size	NHST comparisons			
	N	Mean	SD	Outliers	N	Mean	SD	Outliers	Hedges' g_p [95% CI]	P (equal variance)	P (equal means)	FDR (equal variance)	FDR (equal means)
All species	38	0.0630	0.1674	1	59	0.0266	0.2543	2	0.1609 [-0.2466, 0.5071]	0.0036	0.3967	0.0126	0.4272
No outliers	37	0.0490	0.1452	0	57	0.0539	0.2110	0	0.0258 [-0.3878, 0.4398]	0.0087	0.8946	0.0244	0.8946
									Clinger MTC less variable.				

Table S4: Bivariate SMA slopes and elevations (height above the X -axis), between triple-filtered bill and foot characters (filtered for phylogeny, body size, and elevation above sea level) with 95% confidence intervals, based on mean values, for each species, among 100 alternative phylogenies, with and without outliers. Outliers determined by iterative Grubbs' tests.

Effect sizes (r): < 0.1 negligible; 0.1 small; 0.3 medium; 0.5 large (Cohen 1992a). *Blue fill* indicates effect size $|r| > 0.1$ and the CI for r does not overlap zero. *Red font* indicates SMA adjusted for measurement error in both variables (Warton et al. 2012), used for all comparisons of slopes and elevations and effect sizes; *black font* indicates no adjustment for measurement error. The effect of measurement error on slopes was about 3%. *Grey fill* indicates that the confidence interval for r spans zero. *Yellow fill* indicates $P(r) \leq 0.05$; *orange fill* indicates the FDR (False Discovery Rate) ≤ 0.05 ; FDR treats all P -values in this table as a family of results. *Green fill* indicates non-overlapping confidence intervals for SMA slope between clingers and non-clingers.

[The table appears on the next two pages.]

Hummingbird Foot Size and Bill Length, Online Supplement p. 23

	Exposed Culmen vs. Tarsus			Exposed Culmen vs. Hallux Claw			Exposed Culmen vs. Middle-toe Claw		
<i>P</i> (Clingers = Non-Clingers)	Slope: <i>P</i> = 0.0001 Elevation: <i>P</i> = 0.0024			Slope: <i>P</i> = 0.0332 Elevation: <i>P</i> = 0.4919			Slope: <i>P</i> = 0.0001 Elevation: <i>P</i> = 0.0062		
<i>FDR</i> (Clingers = Non-Clingers)	Slope: <i>FDR</i> = 0.0072 Elevation: <i>FDR</i> = 0.0328			Slope: <i>FDR</i> = 0.0884 Elevation: <i>FDR</i> = 0.5940			Slope: <i>FDR</i> = 0.0024 Elevation: <i>FDR</i> = 0.0298		
	All species	Clingers	Non-clingers	All species	Clingers	Non-clingers	All species	Clingers	Non-clingers
Sample size (<i>n</i>)	218	65	143	220	66	144	103	38	59
Number of Outliers	5	1	4	1	1	0	1	1	0
SMA Slope	0.912 0.921	-1.333 -1.359	0.755 0.761	-1.242 -1.272	-1.576 -1.626	-1.165 -1.194	1.918 2.026	-2.902 -3.214	1.356 1.408
No outliers	1.034	-1.174	0.928	-1.216	-1.408	-1.194	2.109	-2.648	1.600
Slope Lower CL	0.799 0.807	-1.710 -1.744	0.641 0.646	-1.415 -1.450	-1.992 -2.054	-1.372 -1.406	1.578 1.667	-4.036 -4.468	1.054 1.095
No outliers	0.904	-1.510	0.786	-1.385	-1.776	-1.406	1.728	-3.713	1.230
Slope Upper CL	1.042 1.052	-1.039 -1.059	0.890 0.895	-1.090 -1.117	-1.246 -1.288	-1.989 -1.013	2.331 2.462	-2.086 -2.313	1.745 1.810
No outliers	1.183	-0.913	1.096	-1.067	-1.116	-1.013	2.575	-1.889	2.082
SMA Elevation	0.033 0.032	0.108 0.111	0.108 0.108	0.105 0.106	0.204 0.211	0.120 0.120	0.005 0.001	0.125 0.144	0.157 0.155
No outliers	0.026	0.065	0.115	0.096	0.155	0.120	-0.027	0.025	0.121
Elevation Lower CL	-0.036 -0.036	-0.051 -0.048	0.032 0.033	0.040 0.041	0.066 0.074	0.043 0.043	-0.106 -0.110	-0.099 -0.079	0.048 0.048
No outliers	-0.041	-0.074	0.039	0.035	0.037	0.043	-0.134	-0.152	0.002
Elevation Upper CL	0.103 0.102	0.267 0.269	0.184 0.184	0.171 0.171	0.341 0.348	0.198 0.197	0.116 0.112	0.349 0.369	0.267 0.264
No outliers	0.093	0.206	0.191	0.159	0.273	0.197	0.081	0.202	0.240
<i>r</i> ²	0.0110	0.0002	0.0298	0.0370	0.1034	0.0163	0.0113	0.0131	0.0758
<i>r</i> ² no outliers	0.0077	0.0001	0.0248	0.0415	0.1236	0.0163	0.0012	0.0001	0.0248
<i>P</i> (<i>r</i>)	0.123	0.905	0.039	0.004	0.008	0.128	0.287	0.495	0.035
<i>FDR</i>	0.198	0.967	0.094	0.021	0.033	0.198	0.383	0.594	0.088
<i>P</i> (<i>r</i>) no outliers	0.202	0.944	0.064	0.002	0.004	0.128	0.735	0.944	0.063
<i>FDR</i> no outliers	0.292	0.967	0.129	0.019	0.021	0.198	0.860	0.967	0.129
Effect size (<i>r</i>)	0.1046	-0.0146	0.1727	-0.1922	-0.3215	-0.1275	0.1063	-0.1146	0.2753
CI (<i>r</i>)	-0.028 0.234	-0.257 0.230	0.009 0.327	-0.316 -0.062	-0.522 -0.087	-0.285 0.036	-0.089 0.293	-0.419 0.212	0.021 0.496
Effect size (<i>r</i>) no outliers	0.0878	-0.0084	0.1575	-0.2036	-0.3515	-0.1275	0.0349	-0.0084	0.1575

[Table continues on next page]

Hummingbird Foot Size and Bill Length, Online Supplement p. 24

	Tarsus vs. Hallux Claw			Tarsus vs. Middle-toe Claw			Middle-toe Claw vs. Hallux Claw		
<i>P</i> (Clingers = Non-Clingers)	Slope: <i>P</i> = 0.0656 Elevation: <i>P</i> = 0.0699			Slope: <i>P</i> = 0.9667 Elevation: <i>P</i> = 0.8730			Slope: <i>P</i> = 0.1040 Elevation: <i>P</i> = 0.0211		
<i>FDR</i> (Clingers = Non-Clingers)	Slope: <i>FDR</i> = 0.1290 Elevation: <i>FDR</i> = 0.1290			Slope: <i>FDR</i> = 0.9667 Elevation: <i>FDR</i> = 0.9667			Slope: <i>FDR</i> = 0.1849 Elevation: <i>FDR</i> = 0.0633		
	All species	Clingers	Non-clingers	All species	Clingers	Non-clingers	All species	Clingers	Non-clingers
Sample size (n)	218	65	143	103	38	59	103	38	59
Number of Outliers	4	0	4	4	0	4	0	0	0
SMA Slope	1.361 1.380	1.178 1.192	1.541 1.569	1.874 1.958	1.799 1.943	1.898 1.960	0.756 0.736	0.676 0.637	0.894 0.886
No outliers	1.214	1.240	-1.349	2.062	1.943	2.126	0.633	0.637	0.760
Slope Lower CL	1.194 1.212	0.923 0.934	1.310 1.334	1.558 1.630	1.294 1.400	1.489 1.541	0.627 0.612	0.492 0.466	0.694 0.690
No outliers	1.061	1.061	-1.597	1.703	1.400	1.648	0.520	0.466	0.581
Slope Upper CL	1.551 1.572	1.505 1.522	1.812 1.845	2.556 2.352	2.450 2.697	2.420 2.493	0.912 0.887	0.928 0.870	1.150 1.137
No outliers	1.389	1.389	-1.141	2.498	2.697	2.744	0.770	0.870	0.996
SMA Elevation	0.011 0.010	-0.066 -0.069	0.035 0.035	-0.143 -0.145	-0.136 -0.145	-0.160 -0.161	0.041 0.041	-0.024 -0.019	0.085 0.084
No outliers	0.014	0.013	0.016	-0.144	-0.145	-0.157	0.050	-0.019	0.096
Elevation Lower CL	-0.060 -0.059	-0.180 -0.179	-0.064 -0.062	-0.237 -0.237	-0.274 -0.279	-0.301 -0.297	-0.010 -0.006	-0.097 -0.083	0.003 0.007
No outliers	-0.051	-0.051	-0.074	-0.229	-0.279	-0.282	0.007	-0.083	0.025
Elevation Upper CL	0.083 0.081	0.045 0.042	0.134 0.132	-0.048 -0.054	0.001 -0.012	-0.018 -0.023	0.092 0.088	0.047 0.044	0.167 0.161
No outliers	0.079	0.079	0.105	-0.059	-0.012	-0.033	0.093	0.044	0.167
<i>r</i>²	0.0466	0.0367	0.0413	0.1095	0.0225	0.1458	0.0860	0.0893	0.0778
No outliers	0.0041	0.0073	0.000	0.0687	0.0189	0.1041	0.0206	0.0893	0.0002
<i>P</i>(<i>r</i>)	0.012	0.198	0.051	0.012	0.520	0.021	0.021	0.129	0.088
<i>FDR</i>	0.012	0.205	0.051	0.012	0.520	0.021	0.021	0.136	0.090
<i>P</i>(<i>r</i>) no outliers	0.213	0.213	0.952	0.009	0.412	0.016	0.156	0.068	0.928
<i>FDR</i> no outliers	0.292	0.292	0.967	0.033	0.520	0.051	0.234	0.129	0.967
Effect size (<i>r</i>)	0.2159	0.1915	0.2032	0.3309	0.1374	0.3818	0.2933	0.2988	0.2789
CI (<i>r</i>)	0.086 0.339	-0.054 0.415	0.041 0.355	0.147 0.492	-0.190 0.437	0.140 0.581	0.106 0.460	-0.023 0.564	0.025 0.499
Effect size (<i>r</i>) no outliers	0.0852	0.0852	-0.0054	0.2621	0.1374	0.3227	0.1434	0.2988	0.0128

Table S5: Bill, foot, and wing allometry, with 95% confidence intervals, computed with SMA based on phylogenetically filtered PGLS scores (mean values, for each species, among 100 alternative phylogenies), with and without statistical outliers. Outliers determined by iterative Grubbs' tests. (Neither hallux claw, nor middle-toe claw, nor weight had any statistical outliers.) The 95% confidence interval for slope excludes isometry (0.33) for all characters, when all species are considered. (For middle-toe claw, clingers $r = 0.398$, CI = [0.323, 0.489]). "SMA Elevation" means height above the X -axis.

Effect sizes (r): < 0.1 negligible; 0.1 small; 0.3 medium; 0.5 large (Cohen 1992a). *Blue fill* indicates effect size $|r| > 0.1$ and the CI for r does not overlap zero. *Red font* indicates SMA adjusted for measurement error in both variables (Warton et al. 2012), used for all comparisons of slopes and elevations and effect sizes; *black font* indicates no adjustment for measurement error. The effect of measurement error on slopes was about 3%. *Grey fill* indicates that the confidence interval for r spans zero. *Yellow fill* indicates $P(r) \leq 0.05$; *orange fill* indicates the FDR (False Discovery Rate) ≤ 0.05 ; FDR treats all P -values in this table as a family of results. *Green fill* indicates non-overlapping confidence intervals for SMA slope between clingers and non-clingers.

[The table appears on the next two pages.]

Hummingbird Foot Size and Bill Length, Online Supplement p. 26

	Exposed Culmen			Tarsus			Hallux Claw		
<i>P</i> (Clingers = Non-Clingers)	Slope: <i>P</i> = 0.1155 Elevation: <i>P</i> = 0.0013			Slope: <i>P</i> = 0.1077 Elevation: <i>P</i> = 0.4591			Slope: <i>P</i> = 0.6676 Elevation: <i>P</i> = 0.2193		
<i>FDR</i> (Clingers = Non-Clingers)	Slope: <i>FDR</i> = 0.1492 Elevation: <i>FDR</i> = 0.0024			Slope: <i>FDR</i> = 0.1452 Elevation: <i>FDR</i> = 0.5075			Slope: <i>FDR</i> = 0.6899 Elevation: <i>FDR</i> = 0.2615		
	All species	Clingers	Non-clingers	All species	Clingers	Non-clingers	All species	Clingers	Non-clingers
Sample size (<i>n</i>)	220	66	144	220	66	144	220	66	144
Number of Outliers	1	1	0	4	0	4	0	0	0
SMA Slope	0.762 0.776	0.874 0.879	0.718 0.722	0.746 0.760	0.642 0.637	0.802 0.800	0.560 0.551	0.548 0.539	0.518 0.508
No outliers	0.734	0.769		0.648		0.662			
Slope Lower CL	0.683 0.687	0.708 0.713	0.630 0.633	0.656 0.669	0.512 0.508	0.681 0.680	0.494 0.487	0.441 0.434	0.441 0.433
No outliers	0.658	0.624		0.571		0.563			
Slope Upper CL	0.850 0.854	1.079 1.084	0.819 0.823	0.848 0.864	0.806 0.799	0.943 0.941	0.634 0.624	0.681 0.668	0.608 0.597
No outliers	0.819	0.949		0.736		0.779			
SMA Elevation	0.001 0.001	-0.164 -0.165	0.071 0.071	0.006 0.005	-0.020 -0.019	0.024 0.024	0.004 0.004	0.053 0.054	-0.006 -0.006
No outliers	-0.006	-0.171		-0.001		0.005			
Elevation Lower CL	-0.057 -0.057	-0.293 -0.293	0.005 0.006	-0.067 -0.069	-0.127 -0.123	-0.080 -0.079	-0.048 -0.046	-0.033 -0.028	-0.072 -0.070
No outliers	-0.061	-0.282		-0.062		-0.078			
Elevation Upper CL	0.059 0.058	-0.035 -0.037	0.136 0.136	0.080 0.078	0.087 0.086	0.128 0.126	0.056 0.054	0.138 0.136	0.060 0.058
No outliers	0.049	-0.059		0.061		0.088			
<i>r</i>²	0.323	0.280	0.366	0.082	0.172	0.042	0.128	0.226	0.049
<i>r</i>² no outliers	0.324	0.288		0.112		0.064			
<i>P</i> (<i>r</i>)	2.22 e-16	3.83 e-06	2.46 e-15	2.74 e-05	0.001	0.015	1.19 e-08	1.79 e-05	0.004
<i>FDR</i>	9.83 e-16	8.48 e-06	9.53 e-15	5.30 e-05	0.003	0.021	4.10 e-08	3.70 e-05	0.006
<i>P</i> (<i>r</i>) no outliers	2.22 e-16	3.14 e-06		1.63 e-06		0.003			
<i>FDR</i> no outliers	9.831 e-16	7.488 e-06		4.21 e-06		0.005			
Effect size (<i>r</i>)	0.5681	0.5287	0.6052	0.2865	0.4150	0.2040	0.3574	0.4755	0.2217
CI(<i>r</i>)	0.472 0.651	0.329 0.683	0.491 0.699	0.160 0.403	0.191 0.598	0.042 0.356	0.237 0.469	0.264 0.643	0.061 0.371
Effect size (<i>r</i>) no outliers	0.5692	0.5368		0.3344		0.2535			

[The table continues on the next page.]

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	Middle-toe Claw			Wing		
<i>P</i> (Clingers = Non-Clingers)	Slope: <i>P</i> = 0.9700 Elevation: <i>P</i> = 0.4218			Slope: <i>P</i> = 0.4748 Elevation: <i>P</i> = 0.1736		
<i>FDR</i> (Clingers = Non-Clingers)	Slope: <i>FDR</i> = 0.9700 Elevation: <i>FDR</i> = 0.4843			Slope: <i>FDR</i> = 0.5075 Elevation: <i>FDR</i> = 0.2153		
	All species	Clingers	Non-clingers	All species	Clingers	Non-clingers
Sample size (<i>n</i>)	103	38	59	220	66	144
Number of Outliers	0	0	0	1	0	1
SMA Slope	0.420 0.403	0.420 0.398	0.420 0.400	0.529 0.531	0.541 0.543	0.509 0.511
No outliers				0.507		0.486
Slope Lower CL	0.354 0.341	0.337 0.323	0.323 0.312	0.489 0.491	0.471 0.475	0.459 0.462
No outliers				0.467		0.437
Slope Upper CL	0.498 0.477	0.525 0.489	0.531 0.512	0.574 0.575	0.622 0.622	0.565 0.566
No outliers				0.550		0.540
SMA Elevation	-0.045 -0.044	0.025 -0.022	-0.060 -0.060	0.001 0.001	-0.006 -0.007	0.008 0.008
No outliers				0.001		0.010
Elevation Lower CL	-0.097 -0.093	-0.087 -0.076	-0.143 -0.138	-0.027 -0.026	-0.055 -0.053	-0.027 -0.026
No outliers				-0.025		-0.022
Elevation Upper CL	0.007 0.005	0.036 0.033	0.022 0.019	0.028 0.027	0.042 0.040	0.042 0.042
No outliers				0.026		0.042
<i>r</i>²	0.247	0.559	0.102	0.640	0.686	0.609
<i>r</i>² no outliers				0.611		0.579
<i>P</i>(<i>r</i>)	1.20e-07	6.33e-08	0.0150	2.22e-16	2.22e-16	2.22e-16
<i>FDR</i>	3.38e-07	1.96e-07	0.0211	9.83e-16	9.83e-16	9.83e-16
<i>P</i>(<i>r</i>) no outliers				2.22e-16		2.22e-16
<i>FDR</i> no outliers				9.83e-16		9.83e-16
Effect size (<i>r</i>)	0.4974	0.7475	0.3196	0.8001	0.8285	0.7803
CI(<i>r</i>)	0.337 0.630	0.563 0.861	0.070 0.532	0.747 0.843	0.734 0.891	0.714 0.841
Effect size (<i>r</i>) no outliers				0.7814		0.7611

Table S6: Bill, foot, and wing allometry, with confidence intervals, computed with OLS based on phylogenetically filtered PGLS scores (mean values, for each species, among 100 alternative phylogenies), taking measurement error variance for body mass into account (method of moments [Warton et al. 2012]). “OLS Elevation” means height above the X -axis. Summary statistics (r^2 , P , FDR , and effect size) from Table S5. *Effect sizes* (r): < 0.1 negligible; 0.1 small; 0.3 medium; 0.5 large (Cohen 1992a).

In *Bivariate relations between traits, including allometry, for clingers vs. non-clingers* (Main text), we explain why we consider OLS inappropriate for estimating allometric slopes.

	Exposed Culmen			Tarsus			Hallux Claw		
	All species	Clingers	Non-clingers	All species	Clingers	Non-clingers	All species	Clingers	Non-clingers
Sample size (n)	220	66	144	220	66	144	220	66	144
OLS Slope	0.444	0.482	0.441	0.216	0.264	0.168	0.211	0.288	0.122
Slope Lower CL	0.358	0.295	0.345	0.119	0.106	0.037	0.143	0.169	0.041
Slope Upper CL	0.529	0.670	0.537	0.313	0.422	0.298	0.278	0.407	0.202
OLS Elevation	-0.001	-0.095	0.052	0.001	0.039	-0.017	0.002	0.096	-0.033
Elevation Lower CL	-0.053	-0.208	-0.007	-0.058	-0.056	-0.097	-0.039	0.024	-0.082
Elevation Upper CL	0.050	0.019	0.111	0.060	0.135	0.063	0.043	0.168	0.015
r^2	0.323	0.280	0.366	0.082	0.172	0.042	0.128	0.226	0.049
$P(r)$	2.22 e-16	3.83 e-06	2.46 e-15	2.74 e-05	0.002	0.014	1.19 e-08	1.79 e-05	0.004
FDR	9.83 e-16	8.48 e-06	9.53 e-15	5.30 e-05	0.003	0.021	4.10 e-08	3.70 e-05	0.006
Effect size (r)	0.5681	0.5287	0.6052	0.2865	0.4150	0.2040	0.3574	0.4755	0.2217
CI(r)	0.472 0.651	0.329 0.683	0.491 0.699	0.160 0.403	0.191 0.598	0.042 0.356	0.237 0.469	0.264 0.643	0.061 0.371

[The table continues on the next page.]

	Middle-toe Claw			Wing		
	All species	Clingers	Non-clingers	All species	Clingers	Non-clingers
Sample size (<i>n</i>)	103	38	59	220	66	144
OLS Slope	0.211	0.320	0.132	0.434	0.453	0.410
Slope Lower CL	0.142	0.236	0.031	0.393	0.383	0.358
Slope Upper CL	0.279	0.405	0.233	0.475	0.522	0.462
OLS Elevation	-0.025	-0.005	-0.040	0.000	0.010	0.001
Elevation Lower CL	-0.067	-0.057	-0.104	-0.025	-0.032	-0.031
Elevation Upper CL	0.018	0.047	0.025	0.025	0.052	0.032
r^2	0.247	0.559	0.102	0.640	0.686	0.609
$P(r^2)$	1.20e-07	6.33e-08	0.0150	2.22e-16	2.22e-16	2.22e-16
<i>FDR</i>	3.38e-07	1.96e-07	0.0211	9.83e-16	9.83e-16	9.83e-16
Effect size (<i>r</i>)	0.4974	0.7475	0.3196	0.8001	0.8285	0.7803
CI(<i>r</i>)	0.337 0.630	0.563 0.861	0.070 0.532	0.747 0.843	0.734 0.891	0.714 0.841

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Table S7: Univariate analysis of phylo-filtered body mass for clingers vs. non-clingers. Effect size is Hedges' g_p . Effect sizes (g_p): small 0.2, medium 0.5, large 0.8 (Cohen 1992a). P (equal variances) determined by F -test. P (equal means) determined by t -test. *Yellow highlight indicates higher value* for results with Effect Size > 0.3 and CI not spanning zero, and/or P or FDR < 0.05. There were no outliers for body mass.

Body mass	Clingers				Non-clingers				Effect Size	Comparison	
	N	Mean	SD	Outliers	N	Mean	SD	Outliers	Hedges' g_p [95% CI]	P(Equal Variance)	P(Equal Means)
All species	66	0.1717	0.5948	0	144	-0.0669	0.6163	0	0.3900 [0.0971, 0.6847]	0.3690	0.0092
Clinger body mass greater than non-clinger body mass											

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Table S8: Univariate analysis of triple-filtered data for the Coquette clade vs. pooled non-Coquette clades, comparing bill and foot elements for clingers vs. non-clingers. Outliers significant at $P < 0.05$ were determined by iterative Grubbs' test. Effect size is Hedges' g_p . Effect sizes (g_p): small 0.2, medium 0.5, large 0.8 (Cohen 1992a). P (equal variances) determined by F -test. P (equal means) determined by t -test (for unequal variances, if necessary). False discovery rate (FDR) computed for all P -values in this table, as a family of results. *Yellow highlight indicates higher value for results with Effect Size > 0.3 and CI not spanning zero, and/or P or $FDR < 0.05$.*

Coquettes Bill	Coquettes Clingers				Coquettes Non-clingers				Effect Size	NHST comparisons			
	N	Mean	SD	Outliers	N	Mean	SD	Outliers	Hedges' g_p [95% CI]	P (equal variance)	P (Equal Means)	FDR (equal variance)	FDR (equal means)
All species	29	-0.0698	0.5296	0	12	0.0756	0.6133	1	0.2751 [-0.4147, 0.9358]	0.2912	0.4518	0.3640	0.4762
Clinger and non-clinger bills do not differ significantly.													
Coquettes Hallux Claw	Coquettes Clingers				Coquettes Non-clingers				Effect Size	NHST comparisons			
	N	Mean	SD	Outliers	N	Mean	SD	Outliers	Hedges' g_p [95% CI]	P (equal variance)	P (Equal Means)	FDR (equal variance)	FDR (equal means)
All species	29	0.1703	0.2682	0	12	-0.0710	0.4254	0	0.7384 [0.0554, 1.4415]	0.0308	0.0887	0.0953	0.1647
Clinger hallux claws longer (by ES), less variable.													
Non-Coquettes Bill	Non-Coquettes Clingers				Non-Coquettes Non-clingers				Effect Size	NHST comparisons			
	N	Mean	SD	Outliers	N	Mean	SD	Outliers	Hedges' g_p [95% CI]	P (equal variance)	P (Equal Means)	FDR (equal variance)	FDR (equal means)
All species	36	0.0294	0.3623	1	132	0.1327	0.3252	0	0.3014 [-0.0673, 0.6780]	0.2093	0.0988	0.2990	0.1647
No outliers	35	-0.0184	0.2187	0	132	0.1327	0.3252	0	0.4858 [0.1132, 0.8714]	0.0032	0.0016	0.0160	0.0160
Clinger bills shorter and less variable, without outlier <i>Ensifera</i> .													
Non-Coquettes Hallux Claw	Non-Coquettes Clingers				Non-Coquettes Non-clingers				Effect Size	NHST comparisons			
	N	Mean	SD	Outliers	N	Mean	SD	Outliers	Hedges' g_p [95% CI]	P (equal variance)	P (Equal Means)	FDR (equal variance)	FDR (equal means)
All species	36	0.1132	0.2918	0	132	-0.0008	0.2930	0	0.5990 [0.2300, 0.9838]	0.4762	0.0381	0.4762	0.0953
Clinger hallux claws longer, less variable.													

Table S9: Bivariate SMA slopes and elevations (height above the X -axis), between bill length (exposed culmen) and hallux claw (filtered for phylogeny, body size, and elevation above sea level), for the Coquette clade, pooled non-Coquette clades, and (from Table S4) all species, with 95% confidence intervals, based on mean values, for each species, among 100 alternative phylogenies, with and without outliers. Outliers determined by iterative Grubbs' tests. All slopes and elevations adjusted for measurement error in both variables (Warton et al. 2012).

Effect sizes (r): < 0.1 negligible; 0.1 small; 0.3 medium; 0.5 large (Cohen 1992a). *Blue fill* indicates effect size $|r| > 0.1$ and the CI for r does not overlap zero. *Grey fill* indicates that the confidence interval for r spans zero. *Yellow fill* indicates $P(r) \leq 0.05$; *orange fill* indicates the FDR (False Discovery Rate) ≤ 0.05 , taking all tests in this table into account (with the exception of the "All Species" columns, repeated from Table S4.) SMA, adjusted for measurement error in both variables (Warton et al. 2012), was used for all comparisons of slopes and elevations and effect sizes.

[The table appears on the next page.]

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	Coquette Clade Exposed Culmen vs. Hallux Claw			Non-Coquette Clades Exposed Culmen vs. Hallux Claw			All Species Exposed Culmen vs. Hallux Claw		
<i>P</i> (Clingers = Non-Clingers)	Slope: <i>P</i> = 0.3450 Elevation: <i>P</i> = 0.2831			Slope: <i>P</i> = 0.5493/0.0309 Elevation: <i>P</i> = 0.7252			Slope: <i>P</i> = 0.0815 Elevation: <i>P</i> = 0.5384		
<i>FDR</i> (Clingers = Non-Clingers)	Slope: <i>FDR</i> = 0.4938 Elevation: <i>FDR</i> = 0.4600			Slope: <i>FDR</i> = 0.5951/0.1339 Elevation: <i>FDR</i> = 0.7252			Slope: <i>FDR</i> = 0.1630 Elevation: <i>FDR</i> = 0.6153		
	All Co- quettes	Clingers	Non- clingers	All non-Co- quettes	Clingers	Non- clingers	All species	Clingers	Non- clingers
Sample size (<i>n</i>)	41	29	12	179	37	132	220	66	144
Number of Outliers	0	0	0	1	1	0	1	1	0
SMA Slope	-1.682	-2.047	-1.461	-1.131	-1.276	-1.168	-1.272	-1.626	-1.139
No outliers				-0.105	-0.753		-1.216	-1.408	-1.194
Slope Lower CL	-2.250	-2.854	-2.768	-1.310	-1.781	-1.387	-1.450	-2.054	-1.353
No outliers				-1.216	-1.053		-1.385	-1.776	-1.406
Slope Upper CL	-1.257	-1.469	-0.771	-0.976	-0.915	-0.983	-1.117	-1.288	-0.960
No outliers				-0.906	-0.539		-1.067	-1.116	-1.013
SMA Elevation	0.140	0.279	-0.028	0.107	0.174	0.131	0.106	0.211	0.132
No outliers				0.096	0.068		0.096	0.155	0.120
Elevation Lower CL	-0.057	0.045	-0.541	0.040	-0.007	0.055	0.041	0.074	0.057
No outliers				0.035	-0.030		0.035	0.037	0.043
Elevation Upper CL	0.338	0.512	0.485	0.173	0.341	0.208	0.171	0.348	0.206
No outliers				0.158	0.166		0.159	0.273	0.197
<i>r</i>²	0.1598	0.2452	0.0579	0.0090	0.0200	0.0389	0.0370	0.1034	0.0163
No outliers				0.0116	0.0511		0.0415	0.1236	0.0163
<i>P</i>(<i>r</i>)	0.010	0.006	0.453	0.206	0.407	0.250	0.004	0.008	0.128
<i>FDR</i>	0.065	0.065	0.535	0.460	0.460	0.460	0.021	0.033	0.198
<i>P</i>(<i>r</i>) no outliers				0.155	0.250		0.002	0.004	0.128
<i>FDR</i> no outliers				0.560	0.521		0.019	0.021	0.198
Effect size (<i>r</i>)	-0.3997	-0.4952	-0.2406	-0.0948	-0.1414	-0.1972	-0.1922	-0.3215	-0.1275
CI (<i>r</i>)	-0.629 -0.105	-0.729 -0.158	-0.715 0.386	-0.238 0.052	-0.445 0.191	-0.493 0.140	-0.316 -0.062	-0.522 -0.087	-0.285 0.036
Effect size (<i>r</i>) no outliers			-	-0.1075	-0.1972		-0.2036	-0.3515	-0.1275

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Table S10: Mean elevation above sea level for clingers vs. non-clingers for all species, for the Coquette clade, and for pooled non-Coquette clades. No significant ($P < 0.05$) elevation outliers were present in any dataset or subset, by iterative Grubbs' test. Effect size is Hedges' g_p . Effect sizes (g_p): small 0.2, medium 0.5, large 0.8 (Cohen 1992a). P (equal variances) determined by F -test. P (equal means) determined by t -test (for unequal variances, if necessary). False discovery rate (FDR) computed for all P -values in this table, as a family of results. Yellow highlight indicates results significant at P or $FDR < 0.05$, and *higher* value is highlighted, where differences are significant.

All species Elevation	All Species Clingers				All Species Non-clingers				Effect Size	NHST comparisons			
	N	Mean	SD	Outliers	N	Mean	SD	Outliers	Hedges' g_p [95% CI]	P (Equal Variance)	P (Equal Means)	FDR (equal variance)	FDR (equal means)
	66	1904	1216	0	144	1105	862	0	0.8073 [0.5124, 1.1190]	0.0004	5.59E-6	0.0018	3.354 E-05
										Clingers live at higher and more-variable elevations than non-clingers			
Non-Coquettes Elevation	Non-Coquettes Clingers				Non-Coquettes Non-clingers				Effect Size	NHST comparisons			
	N	Mean	SD	Outliers	N	Mean	SD	Outliers	Hedges' g_p [95% CI]	P (Equal Variance)	P (Equal Means)	FDR (equal variance)	FDR (equal means)
	37	1543	1122	0	132	1064	798	0	0.5441 [0.1793, 0.9232]	0.0037	0.0188	0.0074	0.0282
										Non-Coquette clingers live at higher and more-variable elevations than non-clingers			
Coquettes Elevation	Coquettes Clingers				Coquettes Non-clingers				Effect Size	NHST comparisons			
	N	Mean	SD	Outliers	N	Mean	SD	Outliers	Hedges' g_p [95% CI]	P (Equal Variance)	P (Equal Means)	FDR (equal variance)	FDR (equal means)
	29	2364	1193	0	12	1561	1350	0	0.6357 [-0.0374, 1.3820]	0.3256	0.0662	0.3256	0.0794
										Coquette clingers live at higher elevations than non-clingers, with a medium-to-large effect size that barely includes 0; $P = 0.07$, $FDR = 0.08$. For the <i>a priori</i> directional hypothesis, $P = 0.0311$.			

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Table S11: Univariate analysis on triple-filtered data for males and females. Bill and foot elements are compared for clingers vs. non-clingers, with and without outliers, for females and for males. Outliers significant at $P < 0.05$ were determined by iterative Grubbs' test. Effect size is Hedges' g_p . Effect sizes (g_p): small 0.2, medium 0.5, large 0.8 (Cohen 1992a). P (equal variances) determined by F -test. P (equal means) determined by t -test (for unequal variances, if necessary). False discovery rate (FDR) computed for all P -values in this table, as a family of results. Yellow highlight indicates results significant at P or $FDR < 0.05$, and *higher* value is highlighted, where differences are significant.

Females Bill	Clingers				Non-clingers				Effect Size	NHST comparisons			
	N	Mean	SD	Outliers	N	Mean	SD	Outliers	Hedges' g_p [95% CI]	P (equal variance)	P (Equal Means)	FDR (equal variance)	FDR (equal means)
All species	57	-	0.4516	1	105	0.1532	0.3248	0	-0.46 [-0.789, -0.141]	0.0049	0.0110	0.0225	0.0244
No outliers	56	-	0.3959	0	105	0.1532	0.3248	0	-0.577 [-0.907, -0.251]	0.0453	0.0012	0.0824	0.0080
										Female clinger bills shorter and more variable than female non-clinger bills			
Females Hallux Claw	Clingers				Non-clingers				Effect Size	NHST comparisons			
	N	Mean	SD	Outliers	N	Mean	SD	Outliers	Hedges' g_p [95% CI]	P (equal variance)	P (Equal Means)	FDR (equal variance)	FDR (equal means)
All species	58	0.1387	0.3578	1	106	-0.0107	0.3382	0	0.431 [0.106, 0.758]	0.3183	0.0088	0.3537	0.0225
No outliers	57	0.1125	0.2992	0	106	-0.0107	0.3382	0	0.377 [0.054, 0.703]	0.1478	0.0221	0.2111	0.0442
										Female clinger hallux claws longer than female non-clinger claws, equally variable			
Females Tarsus	Clingers				Non-clingers				Effect Size	NHST comparisons			
	N	Mean	SD	Outliers	N	Mean	SD	Outliers	Hedges' g_p [95% CI]	P (equal variance)	P (Equal Means)	FDR (equal variance)	FDR (equal means)
All species	58	0.1008	0.2819	0	106	0.0265	0.5210	3	0.164 [-0.156, 0.485]	<0.001	0.3140	0.0010	0.3537
No outliers	58	0.1008	0.2819	0	103	0.0743	0.4448	0	0.067 [-0.255, 0.389]	0.0001	0.6824	0.0010	0.6824
										Female clinger tarsus equally as long as female non-clinger tarsus, less variable			

[The table continues on the next page.]

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Males Bill	Clingers				Non-clingers				Effect Size	NHST comparison			
	N	Mean	SD	Outliers	N	Mean	SD	Outliers	Hedges' g_p [95% CI]	P (equal variance)	P (Equal Means)	FDR (equal variance)	FDR (equal means)
All species	55	0.0025	0.4457	2	114	0.1374	0.3346	0	0.350 [0.048, 0.661]	0.0062	0.0498	0.0225	0.0830
No outliers	53	-0.0102	0.3356	0	114	0.1374	0.3346	0	0.434 [0.131, 0.747]	0.0910	0.0088	0.1400	0.0225
									Male clinger bills shorter than male non-clinger bills, equally variable without outlier <i>Ensifera</i>				
Males Hallux Claw	Clingers				Non-clingers				Effect Size	NHST comparisons			
	N	Mean	SD	Outliers	N	Mean	SD	Outliers	Hedges' g_p [95% CI]	P (equal variance)	P (Equal Means)	FDR (equal variance)	FDR (equal means)
All species	55	0.1385	0.3527	0	114	-0.0166	0.3904	0	0.405 [0.082, 0.731]	0.1744	0.0090	0.2180	0.0225
									Male clinger hallux claws longer than male non-clinger claws, equally variable				
Males Tarsus	Clingers				Non-clingers				Effect Size	NHST comparisons			
	N	Mean	SD	Outliers	N	Mean	SD	Outliers	Hedges' g_p [95% CI]	P (equal variance)	P (Equal Means)	FDR (equal variance)	FDR (equal means)
All species	55	0.0697	0.3671	0	114	0.0372	0.4105	0	0.156 [-0.158, 0.473]	0.1728	0.6177	0.2180	0.6502
									Male clinger tarsus equally as long as male non-clinger tarsus, equally variable				

Table S12: Bivariate SMA slopes and elevations for males and females. Based on triple-filtered bill and foot characters (filtered for phylogeny, body size, and elevation), with confidence intervals, for all species (from Table S4), based on mean values, for each species, among 100 alternative phylogenies, with and without outliers. Outliers determined by iterative Grubbs' tests. (Male Tarsus and Male Hallux Claw had no outliers. Middle-toe claw is not included in this table, as only one specimen per species was measured.) SMA slope and elevation comparisons (top of table) exclude outliers to avoid high leverage on slopes. All analyses take account of measurement error in all variables. "Elevation" means height above the X -axis.

Blue fill indicates effect size $|r| > 0.1$ and the CI for r does not overlap zero. *Effect sizes (r):* < 0.1 negligible; 0.1 small; 0.3 medium; 0.5 large (Cohen 1992a). *Grey fill* indicates that the confidence interval for r spans zero. *Yellow fill* indicates $P(r^2) \leq 0.05$; *orange fill* indicates the FDR (False Discovery Rate) ≤ 0.05 , taking all tests in this table into account.).

[The table appears on the next page.]

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	Exposed Culmen vs. Tarsus			Exposed Culmen vs. Hallux Claw			Tarsus vs. Hallux Claw		
<i>P</i> (Females = Males)	Slope: $P = 0.5570$ Elevation: $P = 0.4559$			Slope: $P = 0.1016$ Elevation: $P = 0.9797$			Slope: $P = 0.4071$ Elevation: $P = 0.7945$		
<i>FDR</i> (Females = Males)	Slope: $FDR = 0.6406$ Elevation: $FDR = 0.6146$			Slope: $FDR = 0.2829$ Elevation: $FDR = 0.9797$			Slope: $FDR = 0.5852$ Elevation: $FDR = 0.9797$		
	Both sexes	Females	Males	Both sexes	Females	Males	Both sexes	Females	Males
Sample size (<i>n</i>)	218	172	179	220	172	179	218	172	179
Number of Outliers	5	4	2	1	2	2	4	3	0
SMA Slope	0.921	0.855	0.972	-1.272	-1.063	-0.968	1.380	1.245	0.966
No outliers	1.034	0.930	0.872	-1.216	-1.043	-0.869	1.214	1.092	
Slope Lower CL	0.807	0.735	0.839	-1.450	-1.233	-1.122	1.212	1.071	0.863
No outliers	0.904	0.780	0.753	-1.385	-0.212	-1.008	1.061	0.938	
Slope Upper CL	1.052	0.992	1.126	-1.117	-0.918	-0.835	1.572	1.447	1.150
No outliers	1.183	1.082	1.011	-1.067	-0.898	-0.749	1.389	1.271	
SMA Elevation	0.032	0.041	0.042	0.106	0.114	0.105	0.010	0.016	0.031
No outliers	0.026	0.003	0.044	0.096	0.102	0.100	0.014	0.043	
Elevation Lower CL	-0.036	-0.034	-0.032	0.041	0.423	0.029	-0.059	-0.075	-0.038
No outliers	-0.041	-0.070	-0.023	0.035	0.032	0.031	-0.051	-0.040	
Elevation Upper CL	0.102	0.117	0.117	0.171	0.186	0.181	0.081	0.106	0.101
No outliers	0.093	0.076	0.112	0.159	0.171	0.168	0.079	0.126	
r^2	0.0110	0.0144	0.0071	0.0370	0.0404	0.0021	0.0466	0.0049	0.0567
No outliers	0.0077	0.0143	0.0090	0.0415	0.0193	0.0028	0.0041	0.0000	
<i>P</i>(<i>r</i>)	0.123	0.117	0.261	0.004	0.008	0.545	0.012	0.364	0.001
<i>FDR</i>	0.283	0.283	0.429	0.031	0.046	0.641	0.046	0.558	0.023
<i>P</i>(<i>r</i>) no outliers	0.202	0.012	0.208	0.002	0.071	0.481	0.213	0.956	
<i>FDR</i> no outliers	0.377	0.046	0.377	0.023	0.233	0.615	0.377	0.980	
Effect size (<i>r</i>)	0.1046	0.1199	0.0845	-0.1922	-0.2009	-0.0455	0.2159	0.0697	0.2382
CI (<i>r</i>)	-0.028 0.234	-0.030 0.264	-0.062 0.228	-0.316 -0.062	-0.340 -0.053	-0.190 0.101	0.086 0.339	-0.080 0.217	0.095 0.371
Effect size (<i>r</i>) no outliers	0.0878	0.1197	0.0951	-0.2036	-0.1390	-0.0533	0.0852	0.0043	
CI (<i>r</i>) no outliers	-0.028 0.234	-0.032 0.266	-0.053 0.239	-0.074 -0.327	-0.283 -0.011	-0.199 0.094	-0.048 0.215	-0.146 0.155	

Table S13: Allometric slopes and elevations (SMA) for males, females, and (from Table S5) both sexes combined, with confidence intervals. All tests based on mean values, for each species, among 100 alternative phylogenies, for phylo-filtered bill and foot characters (filtered for phylogeny only), with and without outliers; outliers determined by iterative Grubbs' tests. SMA slope and elevation comparisons (top of table) exclude outliers to avoid high leverage on slopes. All analyses take account of measurement error in all variables. Middle-toe claw is not included in this table, as only one specimen per species was measured. "Elevation" means height above the X -axis.

Blue fill indicates effect size $|r| > 0.1$ and the CI for r does not overlap zero. *Effect sizes (r):* < 0.1 negligible; 0.1 small; 0.3 medium; 0.5 large (Cohen 1992a). *Yellow fill* indicates $P(r^2) \leq 0.05$; *orange fill* indicates the FDR (False Discovery Rate) ≤ 0.05 , taking all tests in this table into account.

[The table appears on the next page.]

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	Exposed Culmen			Tarsus			Hallux Claw		
<i>P</i> (Females = Males)	Slope: <i>P</i> = 0.0562 Elevation: <i>P</i> = 0.8108			Slope: <i>P</i> = 0.0395 Elevation: <i>P</i> = 0.5591			Slope: <i>P</i> = 0.3872 Elevation: <i>P</i> = 0.6263		
<i>FDR</i> (Females = Males)	Slope: <i>FDR</i> = 0.0738 Elevation: <i>FDR</i> = 0.8108			Slope: <i>FDR</i> = 0.0553 Elevation: <i>FDR</i> = 0.6523			Slope: <i>FDR</i> = 0.4783 Elevation: <i>FDR</i> = 0.6922		
	Both sexes	Females	Males	Both sexes	Females	Males	Both sexes	Females	Males
Sample size (<i>n</i>)	220	172	179	220	153	179	220	172	179
Number of Outliers	1	2	1	4	4	0	0	3	0
SMA Slope	0.776	0.810	0.707	0.760	1.033	0.623	0.551	0.704	0.619
No outliers	0.734	0.797	0.670	0.648	0.783			0.676	
Slope Lower CL	0.687	0.713	0.629	0.669	0.880	0.542	0.487	0.610	0.538
No outliers	0.658	0.699	0.595	0.571	0.667			0.585	
Slope Upper CL	0.854	0.921	0.794	0.864	1.123	0.718	0.624	0.814	0.713
No outliers	0.819	0.909	0.752	0.736	0.920			0.782	
SMA Elevation	0.001	0.039	0.025	0.005	0.050	0.013	0.004	-0.003	0.007
No outliers	-0.006	0.027	0.015	-0.001	0.050			-0.016	
Elevation Lower CL	-0.057	-0.027	-0.036	-0.069	-0.075	-0.059	-0.046	-0.074	-0.063
No outliers	-0.061	-0.036	-0.042	-0.062	-0.038			-0.081	
Elevation Upper CL	0.058	0.106	0.086	0.078	0.178	0.086	0.054	0.068	0.080
No outliers	0.049	0.091	0.074	0.061	0.140			0.049	
<i>r</i>²	0.3230	0.2742	0.3687	0.0820	0.0005	0.0912	0.1280	0.0741	0.0949
No outliers	0.324	0.2430	0.3776	0.112	0.0289			0.0825	
<i>P</i>(<i>r</i>)	3.36 e-20	1.69 e-13	1.98 e-19	1.59 e-05	0.7901	3.98 e-05	4.98 e-08	0.0003	2.72 e-05
<i>FDR</i>	3.53 e-19	7.10 e-13	1.04 e-18	3.71 e-05	0.8108	7.60 e-05	1.49 e-07	0.0005	5.71 e-05
<i>P</i>(<i>r</i>) no outliers	2.74 e-20	8.51 e-12	7.30 e-20	4.86 e-07	0.0383			0.0002	
<i>FDR</i> no outliers	2.53 e-19	2.98 e-11	5.11 e-19	1.28 e-06	0.0553			0.0004	
Effect size (<i>r</i>)	0.5681	0.5237	0.6074	0.2865	0.0217	0.3020	0.3574	0.2722	0.3081
CI (<i>r</i>)	0.472 0.651	0.406 0.624	0.506 0.692	0.160 0.403	-0.137 0.179	0.163 0.429	0.237 0.469	0.128 0.405	0.170 0.435
Effect size (<i>r</i>) no outliers	0.5692	0.4930	0.6145	0.3344	0.1699			0.2873	
CI (<i>r</i>) no outliers	0.473 0.652	0.370 0.599	0.514 0.698	0.212 0.446	0.010 0.321			0.143 0.420	

Table S14: SMA slopes and elevations between bill length and hallux claw, for raw data (log 10 transformed), not filtered for body size, phylogeny, or elevation, for all species, for clingers, and for non-clingers, with confidence intervals, with and without outliers. Outliers determined by iterative Grubbs' tests. The only outlier was the bill length (exposed culmen) of *Ensifera ensifera*, an atypical clinger. The effect size is negligible (with a CI that overlaps zero), and $P > 0.05$ for all three groupings of species. See Fig. S5. "Elevation" means height above the X -axis.

	Raw data Exposed Culmen vs. Hallux Claw		
	All species	Clingers	Non-clingers
Sample size (n)	220	66	144
Number of Outliers	1	1	0
SMA Slope	-1.2982	-1.4812	1.7083
No outliers	-1.2409	-1.2515	
Slope Lower CL	-1.4829	-1.8938	1.4504
No outliers	-1.4177	-1.6013	
Slope Upper CL	-1.1366	-1.1585	2.0121
No outliers	-1.0862	-0.9781	
SMA Elevation	1.8870	2.0901	0.5657
No outliers	1.8565	1.9492	
Elevation Lower CL	1.8017	1.8756	0.4412
No outliers	1.7751	1.7675	
Elevation Upper CL	1.9722	2.3047	0.6901
No outliers	1.9379	2.1308	
r^2	0.0011	0.0107	0.0183
r^2 no outliers	0.0034	0.0198	
$P(r)$	0.6246	0.4096	0.1053
FDR	0.6246	0.5120	0.5120
$P(r)$ no outliers	0.3907	0.2628	
FDR no outliers	0.5120	0.5120	
Effect size (r)	-0.0332	-0.1033	0.1352
CI(r)	-0.1647 0.0995	-0.3369 0.1423	-0.0290 0.2923
Effect size (r) no outliers	-0.0584	-0.1407	
CI(r) no outliers	-0.1895 0.0748	-0.3701 0.1049	

Supplemental Text

Supplemental Text S1: The functional morphology of clinging.

Supplemental Text S2: *Methods:* Elevation.

Supplemental Text S3: *Methods:* Effect size vs. null hypothesis significance tests (NHSTs).

Supplemental Text S4: Methods and Discussion: Measurement error.

Supplemental Text S5: Bill length vs. hallux claw without filtering.

Supplemental Text S6: Hummingbird body size and allometry: An overview.

Supplemental Text S7: Results for sexes separately.

Supplemental Text S8: *Discussion:* The functional morphology of clinging.

Literature Cited in Supplemental Text

Supplemental Text S1: The Functional Morphology of Clinging

The literature on avian grasping biomechanics has little to say about hummingbirds, but studies of other birds offer some guidance. For example, (Zeffer and Norberg 2003) and (Zeffer et al. 2003) studied the hindlimbs of birds that they distinguished as “climbers” (birds that “climb on vertical surfaces by hopping upwards”) *versus* “hangers” (“species that mainly use their hind limbs to hang underneath branches”). For clinging hummingbirds, unfortunately, data regarding the amount of time spent engaging in each of these behaviors (*e.g.*, Moreno and Carrascal [1993], for *Parus* spp.) are scarce (Igić et al. 2020).

Clinging in relation to toe and claw length. Toe and claw lengths, relative to body size, vary tremendously among avian taxa and play important roles in grasping and clinging behavior (reviewed by Sustaita et al. [2013]). However, the biomechanical implications of differences in toe and claw lengths are not always clear and often depend on substrates and contact angles (Backus et al. 2015; Norberg 1986; Norberg 1979; Winkler and Bock 1976; Zeffer and Norberg 2003). Leisler and Winkler (1985) found that silviid warbler species with excellent clinging abilities have “long legs and (hind) toes,” whereas silviids that use their feet primarily to perch have shorter legs and shorter hind (hallux) toes. Norberg (1979) maintained that “long toes and curved claws are desirable as support in climbing” in *Certhia familiaris* (Eurasian treecreeper).

Relatively longer toes (Backus et al. 2015) and claws (Norberg 1986; Winkler and Bock 1976) can expand the avian foot span, minimizing the horizontal (reaction) forces normal to the substrate that would otherwise pull a clinging bird off the substrate and, thus, the muscle forces required to oppose them (Fig. S1, panels G and H). However, in a broad taxonomic sample of birds (but not including hummingbirds), Pike and Maitland (2004) found no compelling differences in relative claw radius (their measure of claw “size”) among predatory, climbing, perching, or ground-dwelling groups. In contrast, Fowler et al. (2009) suggested that, in raptors, increased claw size might serve as a mechanism for lengthening the entire toe and consequently the reach of the talon, while preserving a relatively high mechanical advantage in the toe, itself, for increased grasping force. Here, we aimed to test the overall prediction that hallux claw length (which, we will show, is correlated with hallux length) should be longer in clingers than in non-clingers, after accounting for body size, phylogeny, and elevation above sea level (Fig. S1, panels G and H).

Clinging and tarsus length. The avian tarsus (technically, the tarsometatarsus) is the third segment of the bird “leg,” formed from fused bones of the foot (Fig. 2). The literature is divided on how tarsus length might be optimized in birds that cling vertically or upside down. On the one hand, studies on a wide array of avian taxa report that clinging and hanging birds should (on biomechanical grounds) and do have shorter legs (*e.g.*, Leisler and Winkler 1985; Moreno and Carrascal 1993; Norberg 1979; Zeffer et al. 2003; Zeffer and Norberg 2003). Shorter tarsi enhance the mechanical advantage of the ankle flexors that act to hold the body close to the substrate (Fig. S1, panels E and F). On the other hand, Stiles (2008) reported that high-elevation Andean hummingbird species, particularly members of the Coquettes clade (Fig. 3)—frequent clingers—tend to have especially long tarsi (as well as large feet and long hallux claws), and Mayr (2015) suggested that the tarsus of swifts is secondarily elongated as an adaptation to vertical clinging in relation to nesting on rock faces and in tree hollows. Weighing the evidence, however, we hypothesized (before analyzing any data) that—after accounting for body size, phylogeny, and elevation above sea level in hummingbirds—clingers would have shorter tarsi than non-clingers (Fig. S1, panels E and F).

Supplemental Text S2: *Methods*: Elevation

Elevation above sea level for each of the 220 species in the full dataset was compiled in one of three ways. For species with elevations recorded on museum specimen tags (primarily relatively recent specimens), the mean elevation for the specimens that we measured for morphological characters was accepted as the most appropriate value, given the potentially elevation-sensitive morphological features we measured. In the absence of such data, mid-elevation (midpoint between upper range limit and lower range limit) was extracted from the literature (citations appear in Appendix 1 of Rangel et al. [2015]). For 23 species lacking both museum specimen tag elevations and authoritative literature elevations, we downloaded the latitude and longitude of the 1000 most recent records (or as many as available, if fewer than 1000) from GBIF (www.gbif.org), but none earlier than 1980, even if 1000 recent records were not available. The minimum sample size was 124 (for *Lophornis pavoninus*, peacock coquette). GBIF's "eliminate doubtful geographical records" option was activated. For each GBIF record, the approximate elevation was recorded by reference to the digital elevation model (DEM) database of WorldClim2 (Fick and Hijmans 2017), and the mean elevation of records was used as the elevation value for the species. We recognize that a few species (*e.g.*, *Patagona gigas*, giant hummingbird) have wide elevational ranges, making elevational midpoint less meaningful than for species with narrow elevational ranges (*e.g.*, *Amazilia boucardi*, mangrove hummingbird), but range midpoint can be far more accurately estimated than elevational range width, which is highly sensitive to sample size.

Supplemental Text S3: *Methods*: Effect size vs. null hypothesis significance tests (NHSTs)

The large sample sizes in our study (up to 220 species, depending on the analysis) offer the statistical power to detect small effects, but risk yielding absurdly tiny *P*-values for null hypothesis significance tests (NHSTs) of strong results (*e.g.*, Tables S5 and S13) (Lin et al. 2013), or yielding marginally "insignificant" results for small samples that nonetheless reveal medium or large effect sizes (*e.g.*, Table S10). Given the established consensus among statisticians (Wasserstein and Lazar 2016) and a growing awareness among biologists

(Nakagawa and Cuthill 2007; Smith 2018) that NHSTs, in general, are often more misleading than informative, we rely in the first instance, on effect size and its confidence intervals (Cohen 1992a; Cohen 1992b; Cumming 2013; Nakagawa and Cuthill 2007), where appropriate measures are available. For completeness, we also report traditional *P*-values (without exception, 2-tailed, regardless of *a priori* predictions). To account for family-wise error rate in the NHST framework, we rely on false discovery rates (FDR), computed with the R function `p.adjust(stats)`, for families of related results (Nakagawa 2004).

Supplemental Text S4: Measurement error

Methods. Because all morphological traits are random variables (not under experimental control), the total variance among species, for any given character, is the sum of measurement error variance and “natural variation” (Smith 2009; Sokal and Rohlf 1995)—the signature of evolutionary divergence among species—also called “natural heterogeneity” (McArdle 2003) or “equation error” (Fuller 2009; Warton et al. 2006)—so called because the true values of variates do not fall exactly along a straight line. The SMA slope is simply the ratio of the standard deviation in *Y* to standard deviation in *X*, with a sign determined by the sign of the correlation coefficient. Thus, without knowing the contribution of (measurement) error variance to the numerator and denominator of this ratio, the slope may be biased in one direction or the other (Smith 2009; Warton et al. 2006). To estimate measurement error for each character (body mass, bill, wing, and foot characters), we first computed the within-species sample variance, among individuals, of log₁₀-transformed measurements for each species in our dataset (Supplemental Spreadsheet S1) for which we had measured 2 or more individuals (sample size ranged from 161 to 222 species, depending on the character). For each character, we combined these variances as a weighted average using Eq. 31 of Warton et al. (2006). For body mass, we used all available museum specimen tag weights (206 species) from our original dataset. Because we measured middle-toe claw for only a single specimen of each of 103 species, measurement error could not be estimated for this character. Where appropriate, we applied the estimated measurement error for hallux claw, as the most reasonable proxy for middle-toe claw.

Results and Discussion. We assessed the role of two sources of error variance that might affect SMA slopes between morphometric characters: within-species, among-individual variance in measured values (an amalgam of sampling error and measurement error) (Clark 2010; Warton et al. 2006) and phylogenetic uncertainty (Rangel et al. 2015). The former seemed substantial enough (averaging about 5% of total variance, Table S2) and variable enough among characters to warrant adjustment of slopes based on the estimated measurement error variances—although doing so had only a negligible effect on results (Tables S4 and S5). Phylogenetic error variance, estimated from PGLS residuals based on samples of 100 alternative phylogenies, as illustrated graphically in Fig. 5, proved to be statistically negligible (Table 2). Clearly, morphological variation among clades and species overwhelms not only within-species variation (including measurement error) but also variation of PGLS residuals among alternative phylogenies.

Supplemental Text S5: Bill length vs. hallux claw without filtering

Without PGLS filtering to neutralize the effects of body size, phylogeny, and elevation, a plot of \log_{10} raw bill length vs. \log_{10} raw hallux claw (Fig. S6) is dominated by the allometric effects of body size on both characters (Figs. 6A and 6C; Table S5), but particularly on hallux claw. Without PGLS filtering, the SMA relations for bill length vs. hallux claw, for clingers, non-clingers, or all species considered together are all negligible (Table S14). Clingers cover virtually the entire scope of hummingbird body size (2.55 g to 21.7 g, Supplemental Spreadsheet S1), and raw log hallux claw is well-correlated with raw log weight ($r = 0.5$). Thus, clingers are spread by the allometric scaling of hallux claw with body size across virtually the entire hallux-claw axis for the raw data of Fig. S5, compared to their concentration in the lower-right quadrant (long hallux claws, short bill) in the triple-filtered data of Fig. 5, demonstrating the essential role of filtering in revealing the functional tradeoff between bill size and hallux claw and its multiple independent origins, independent of body size.

Supplemental Text S6: Hummingbird body size and allometry: An overview

Body size is consistently a master functional trait among species within any animal clade, and hummingbirds are no exception (Bribiesca et al. 2019). The scaling of energy budgets (Groom

et al. 2018; Shankar et al. 2020), territory or home range size (Carpenter et al. 1983; Márquez-Luna et al. 2015; Norton et al. 1982), behavioral dominance (Bribiesca et al. 2019; Pavan et al. 2020), and morphological features all scale with body size. In this study, in order to assess and interpret relations between the size of hummingbird bills and feet, we must do so in relation to body size (mass).

When studying comparative morphology within a clade, it is useful to treat isometric proportions (dimensional similarity [Greenewalt 1975]) as a sort of null model for the relationship of shape with body mass (weight). Suppose we take a photograph of a small hummingbird—say, the 2.5 g male *Selasphorus calliope* (calliope hummingbird) and enlarge it photographically, twofold. Then the larger bird, if it could exist, would be isometric (geometrically or dimensionally similar) with the smaller. Each linear dimension (body length, wing chord, bill length, tarsus length, hallux claw chord, etc.) has been doubled, but since weight scales as the cube of linear dimensions, the larger bird would weigh 8 times as much as the smaller, or 20 g—as much as the largest hummingbird, *Patagona gigas* (giant hummingbird).

Thus, the slope of a log-log plot of linear measurements and body weight is 1/3 for isometric scaling. Any systematic deviations from this slope reveal a pattern of allometry (which Reiss (1989) succinctly called “the study of size and its biological consequences”) between shape and size. In fact, a 20 g isometric version of a male *S. calliope* would be incapable of flight. Its wings would be far too short to create the necessary lift, or it would need to beat them impossibly fast. Because wing area (or wing-disc area, for the helicopter-like aerodynamics of hovering flight [Altshuler et al. 2004b; Epting and Casey 1973; Feinsinger et al. 1979; Greenewalt 1975; Groom et al. 2018; Skandalis et al. 2017]) scales with the square of wing length, the wing-disc area of a giant *S. calliope*—with its eightfold greater weight—would be only four times the wing-area of the actual *S. calliope*. In a striking pattern of constrained allometry, log wing length in hummingbirds scales with log body mass with a slope of about 1/2, maintaining, on average, a constant relation between wing-disc area and body mass over the entire range of body weights—a pattern unique among flying animals (Greenewalt 1975; Groom et al. 2017; Skandalis et al. 2017), although the deviations of individual species from this pattern reflect adaptive variation (Altshuler et al. 2004a; Feinsinger et al. 1979). In this study, then, our

examination of the morphology of hummingbird bills and feet includes an analysis the allometric scaling of each character, as a path towards interpreting function.

Supplemental Text S7: Results for sexes separately

Univariate comparisons, bivariate relationships, and allometric analysis for females and males, separately, proved to be almost entirely concordant with the intersex results. For each sex, clingers have substantially shorter bills and longer hallux claws than non-clingers, but tarsi do not differ between clingers and non-clingers (Table S11), just as for the intersex data (Table S3). In bivariate comparisons (Table S12), males and females do not differ significantly in the slope or the elevation of the SMA relation for culmen *vs.* tarsus., culmen *vs.* hallux claw, or tarsus *vs.* hallux claw. Bill length and hallux claw are negatively correlated for each sex separately, as they are for intersex data, but more strongly for females than males (Table S12).

Table S13 compares allometric results for females and males, separately, with the principal intersex results (except for middle-toe claw, for which we did not have sex-specific data). For tarsus, the allometric SMA slope for females was significantly greater than for males. Slopes for did not differ significantly between the sexes for hallux claw. Slopes for both sexes are positively allometric and highly significant for all three characters; none includes isometry in its confidence interval.

Supplemental Text S8: *Discussion*: The functional morphology of clinging

The prediction of longer hallux claws among clingers (Supplemental Text S1) was strongly confirmed (Tables S3, S8, and S11). The prediction of shorter tarsi among clingers was not: there is no evidence that tarsi differ in length between clingers and non-clingers (Tables S3 and S11). In contrast with hallux claw, middle-toe claw did not differ significantly in length between clingers and non-clingers for triple-filtered data (Table S3). However, middle-toe claw length was significantly less variable among clingers than among non-clingers (Table S3), and not as strongly correlated with hallux claw length among clingers (Figs. 4B and 4C, Table S4). Taken together, these findings indicate that elongation of foot span in clingers is driven largely

by the hallux claw—or hallux toe, including the claw (as for the treecreepers studied by Norberg [1986]).

The ancestral condition for Apodiformes is a relatively long tarsus, which was shortened in the swifts after the split between swifts and hummingbirds (Ksepka et al. 2013). The apparent lack of selection for decreased tarsus length on the hummingbird side of the apodiform tree could arise from two sources. First, birds that cling or hang may benefit from longer distal hindlimbs, which may extend their reach for accessing substrates, such as bracts of pendulous flowers (Stiles 2008). Second, in other birds, such as treecreepers, shortening of the hindlimb occurs in other limb elements (particularly the tibiotarsus), leaving the tarsometatarsus relatively less affected (Norberg 1979). In hummingbirds, the drawbacks of relatively longer tarsi may be compensated by postural changes during clinging, perhaps through greater flexion of the proximal hindlimb joints, bringing the body closer to the substrate, and/or by greater development of the distal hindlimb musculature or their moment arms (Zeffer and Norberg 2003). The negligible relationship between hallux claw and tarsus lengths in clingers, compared to the stronger relation observed in non-clingers (Fig. 4B and 4C; Tables 2 and S5), supports our contention that selection for clinging ability has decoupled the omnibus relationship among hindlimb elements (Fig. 4) that otherwise pervades this family (as well as other bird groups Zeffer et al. [2003]).

In their classic myological study of 7 species of hummingbirds, chosen to represent all major clades, Zusi and Bentz (1984) commented on the “strong development” of hummingbird tarsometatarsal flexors and extensors of the digits, which would enhance their abilities while “perching, clinging vertically, or hanging upside down.” Four of the 7 species they studied happened to be known clingers (Fig. 3 and Supplemental Spreadsheet S1). In two of these (*Metallura tyrianthina*, a Coquette, and *Thalurania furcata*, an Emerald), Zusi and Benz noted that the distal belly of the extensor hallucis longus (a muscle that controls a strong tendon that inserts on dorsal surface of the ungual phalanx of the hallux) is “unusually large for the size of the bird” (Zusi and Bentz 1984). Because our study was limited to length measurements reflective only of external torques, we tacitly assume that muscles, tendons, their origins and insertions, and moment arms scale proportionately (with body size) across species.

Using the tail as a posterior point of contact accomplishes much the same thing by

establishing a broad and stable base (Norberg 1979). In fact, larger clinging hummingbirds, such as *Sephanoides fernandensis* (Juan Fernández firecrown) (Colwell 1989), *Oreotrochilus estella* (Andean hillstar) (Carpenter 1976) and *Oxypogon guerinii* (bearded helmetcrest; Fig. 1, photograph *d*), have been observed to prop their tails against the substrate while clinging, further reducing horizontal forces and the energetic cost of clinging (Norberg 1986; Norberg 1979; Winkler and Bock 1976). Several, but not all, of the hummingbird species that Clark and Rankin (2019) determined to have monomorphic long tails are also known clingers.

It is possible that short-billed species that cling to feed may also use their relatively large feet, to a greater degree than long-billed species, not only during feeding, but also for fighting (AR-G, unpublished data) or for preening, which would complicate the hypothesis that feeding, alone, drives these patterns. With regard to preening, however, Clayton and Cotgreave (1994) predicted the opposite—that long-billed birds would preen with their feet more than short-billed species—because a long bill would be too awkward to reach some feathers (for example, on the head and neck). Indeed, their data supported this prediction, showing that long-billed birds scratch with their feet more than short-billed birds, although their meagre data for hummingbirds (five individuals representing four species) was insufficient to draw any conclusions.

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