

Locomotion and Energetics of Divergent Foraging Strategies in Hummingbirds: A Review

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Abstract

Hummingbirds have two main foraging strategies: territoriality (defending a patch of flowers) and traplining (foraging over routine circuits of isolated patches). Species are often classified as employing one or the other. Not only have these strategies been inconsistently defined within the behavioral literature, but this simple framework also neglects the substantial evidence for flexible foraging behavior displayed by hummingbirds. Despite these limitations, research on hummingbird foraging has explored the distinct avenues of selection that proponents of either strategy presumably face: trapliners maximizing foraging efficiency, and territorialists favoring speed and maneuverability for resource defense. In earlier studies, these functions were primarily examined through wing disc loading (ratio of body weight to the circular area swept out by the wings, WDL) and predicted hovering costs, with trapliners expected to exhibit lower WDL than territorialists and thus lower hovering costs. While these pioneering models continue to play a role in current research, early studies were constrained by modest technology, and the original expectations regarding WDL have not held up when applied across complex hummingbird assemblages. Current technological advances have allowed for innovative research on the biomechanics/energetics of hummingbird flight, such as allometric scaling relationships (e.g., wing area–flight performance) and the link between high burst lifting performance and territoriality. Providing a predictive framework based on these relationships will allow us to reexamine previous hypotheses, and explore the biomechanical trade-offs to different foraging strategies, which may yield divergent routes of selection for quintessential territoriality and traplining. With a biomechanical and morphofunctional lens, here we examine the locomotor and energetic facets that dictate hummingbird foraging, and provide a) predictions regarding the behavioral, biomechanical, and morphofunctional associations with territoriality and traplining;

and b) proposed methods of testing them. By pursuing these knowledge gaps, future research could use a variety of traits to help clarify the operational definitions of territoriality and traplining, to better apply them in the field.

Keywords: foraging ecology, Trochilidae, nectar feeding, plant-pollinator interaction, resource use

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Introduction

A foraging strategy is the summary of an animal's behavioral adaptations that allow it to successfully acquire food (Vogel et al. 2017). In natural habitats, the availability and distribution of resources are continuously in flux, and animals must continually adapt their foraging strategies to meet their dietary needs. As such, these strategies play a vital role in determining fitness and are shaped heavily by natural selection (Hassell and Southwood 1978). Unlike most heterotrophs, nectar-feeding animals exploit an ephemeral, self-replenishing resource that is stationary and relatively predictable during blooming, yet scattered across the landscape at very different scales depending on the plant's reproductive strategy (Janzen 1971; Betts et al. 2015). All of these factors influence the diverse foraging adaptations displayed by nectarivores. Hummingbirds, in particular, stand out as one of the most energetically constrained animals, requiring a copious caloric supply given their ability to perform prolonged hovering, which is one of the most energy-demanding forms of locomotion (Weis-Fogh 1972; Chai and Millard 1997; Suarez and Gass 2002). Hummingbird foraging strategies should reflect this energetic constraint, especially given the variability of flight requirements that contrasting strategies entail, providing a context to understand the links between behavior, biomechanics, performance, and functional morphology.

The majority of research on hummingbird foraging has focused on two functional groups: territorialists and trapliners, which have been treated dichotomously (Feinsinger and Chaplin 1975; Neill 1987; Gill 1988; Cotton 1998a; Hadley et al. 2018; Torres-Vanegas et al. 2019). The concept of territoriality was perhaps first indicated by Aristotle concerning eagles, but proposed more fully by Valli da Todi in 1601, regarding nightingales establishing "freeholds" to dominate and defend from conspecifics (Birkhead 2008). Since Valli da Todi's pioneering work,

territoriality has become a central pillar in behavioral ecology, particularly in birds (Nice 1941; Fretwell and Calver 1969; Greenberg and Gradwohl 1986; Drury et al. 2020), among which hummingbirds have been recognized for their exceptional pugnacity (Lyon et al. 1977; Hixon et al. 1983; Cotton 1998b; Evens and Harper 2020). Territorial hummingbirds face prominent **interference competition** (see Glossary), and will defend large patches of clumped floral resources over an extended period (Fig. 1A) (e.g., Feinsinger and Chaplin 1975; Feinsinger et al. 1979). By threatening or attacking other hummingbirds attempting to feed, territorialists maintain feeding access to a localized source of energy (Stiles 1975; Altshuler, Stiles, et al. 2004). In the case of males, territories and their resources can also be used to attract females (Temeles and Kress 2010), which may utilize alternative foraging strategies such as traplining or **territory parasitism** (see Glossary) (Kodric-Brown and Brown 1978; Temeles et al. 2005).

The term “traplining” was first coined by Janzen (1971 and *pers. comm.*), who likened the systematic foraging of hummingbirds—and the long-distance, periodic foraging sequences of Euglossine bees—to that of a fur trapper checking their line of traps spread across the landscape (Thomson et al. 1997); however, the concept was discussed as early as 1872 by Darwin with reference to bumble bees (Freeman 1968). A traplining hummingbird, occasionally classified as “non-territorial” (Feinsinger and Chaplin 1975; Powers and McKee 1994; Gass and Garrison 1999), faces prominent **exploitative competition** (see Glossary) and will routinely visit flowers widely dispersed across the landscape (Fig. 1B) (e.g., Stiles 1975; Tiebout 1991; Garrison 1995; Volpe et al. 2014). In so doing, trapliners attempt to systematically harvest a flower’s replenished nectar before competitors and (as demonstrated in bumblebees) fly the shortest routes between floral resources to conserve energy (Ohashi et al. 2007). Thus, foraging classifications carry accompanying assumptions about the ways in which a bird will collect,

invest, and expend energy (Powers and McKee 1994; Tello-Ramos et al. 2015). Many scientists have conceded that these broad categories are an oversimplification, but, because they are useful for the purpose of identifying trends (Stiles 1978; Altshuler, Stiles, et al. 2004; Hadley et al. 2018), hummingbirds are generally classified plainly as territorialists or trapliners. Yet as pointed out by Tello-Ramos et al. (2015), these classifications are often established without empirical evidence.

The scant verification of hummingbird traplines is rooted in the logistical challenge of tracking such small, quick birds across large spatial scales. Our understanding of hummingbird traplining is largely based on regularity in floral visitation to a limited subset of flowers (Temeles et al. 2006). However, more recent work has demonstrated that Rufous Hummingbirds (*Selasphorus rufus*), highly territorial and aggressive (Cornell 2017; Healy and Calder 2020), will form visitation circuits on small experimental flower arrays (Tello-Ramos et al. 2015, 2019). Tello-Ramos et al. (2015, 2019) argue that a bird does not need to switch between territoriality and traplining, defining the latter as “foraging behavior where animals repeatedly visit rewarding locations in a predictable sequence.” This seems compatible with how traplining is defined in reference to other taxa (Ohashi and Thomson 2009; Lihoreau et al. 2011, 2013; Woodsworth et al. 1981; Garber 1988; Deygout et al. 2009; Gilbert and Singer 1975). As such, the definition of traplining long applied by hummingbird biologists—i.e. commuting between dispersed resources without defending them (e.g., Linhart 1973; Cotton 1998a; Hadley and Betts 2009; Torres-Vanegas et al. 2019)—is somewhat atypical. Given the ongoing debate and in order to avoid confusion among hummingbird biologists, we elect to equate the term territoriality with **stationary interference**, to reflect a bird’s defense of the resources within a specific area, and

traplining with **traveling interference**, to convey long-distance movements without resource defense (see Glossary and Rico-Guevara et al. this issue).

Our perception of foraging poses a challenge to tease apart, but morphological traits may provide insight into the underpinnings of behavior, by imposing limits on the strategies a bird can physically or successfully employ relative to competitors (Feinsinger et al. 1979). As foraging is a complex trait in hummingbirds, in part due to the aerodynamic and kinematic complexities of forward, backward, turning, and hovering flight (Altshuler and Dudley 2002; Warrick et al. 2005; Tobalske et al. 2007; Sapir and Dudley 2012; Segre et al. 2016; Dakin et al. 2019), variation in wing morphology and body size drives much of the differences in performance, and presumably behavior. However, this research is often purely correlative, as opposed to empirically demonstrating how morphological variability drives foraging decisions under different ecological conditions. Previous work on hummingbirds has attempted to corroborate the relationship between flight morphology and behavior (Feinsinger and Chaplin 1975; Feinsinger et al. 1979), but the basis of these relationships is contentious (Altshuler, Stiles et al. 2004). Examining the patterns between hummingbird morphology and foraging strategies will likely shed light on why each individual, sex, or species performs the way it does in specific competitive skills or under particular energetic constraints. Here, we bring together our contemporary knowledge of the aerodynamics of hummingbird flight and attempt to reconcile it with the complexity of their foraging behaviors, to begin to piece together the current state of the field.

To do so, it is important to take an integrative approach, examining not only behavior and ecology, but also the physical mechanisms associated with each foraging strategy. In short, at what must a territorial or traplining hummingbird excel for their preferred strategy to be

successful under the kind of competition (i.e. interference/exploitation) they face more frequently? Or, for a hummingbird with a given set of morphofunctional traits, which strategy yields higher rewards under a given competitive context? As the interplay between natural and sexual selection is complex, topics such as bill morphology, coloration, breeding strategies, and vocalizations warrant separate and thorough treatment outside of the scope of this paper. Here, to assess how form and function together determine hummingbird locomotion and energetics, we will: 1) Discuss the flexibility of nectar-foraging behaviors, and environmental factors that dictate changes in behavior; 2) In the context of energetics, review body size and aerodynamic models as they relate to foraging and flight, and outline testable predictions regarding how selection might influence the various foraging strategies; and 3) Conclude with a general discussion of remaining knowledge gaps, and highlight the value in clarifying our operational definitions of hummingbird foraging strategies.

Energetics and Competition Yield Flexible Foraging

Despite the fact that territoriality and traplining have garnered the majority of hummingbird biologists' attention, a number of other nectar-foraging strategies have been proposed for this speciose group of birds (over 330 species) (McGuire et al. 2014). As the given foraging strategy of an individual hummingbird depends on factors that are both fixed (e.g., species and/or sex) and contextual (e.g., resource distribution, latitude, altitude, opportunity given the absence or subordination of competitors, and time of day or year), it is helpful to review these additional strategies (Stiles 1985; Altshuler and Dudley 2002; Altshuler 2006).

Feinsinger and Colwell suggested in 1978 that five major nectar-foraging categories exist among

hummingbirds: 1) **territorialists**; 2) **high-reward trapliners**; 3) **low-reward trapliners**; 4) territory parasites, broken into **filchers** (small hummingbirds parasitizing fringes of an individual's territory) and **marauders** (large hummingbirds able to withstand territorialist attacks in order to parasitize its resources); and 5) **generalists** (see Glossary for definitions). Feinsinger (1976) has also described **haphazard foraging** (see Glossary), suitable for areas with flowers in greater abundance but lower diversity, yet the distinction from generalism is somewhat unclear (Garrison 1995). Though Feinsinger and Colwell's terms provided a useful initial framework, assigning specific hummingbirds to these categories has been difficult, and thus these classifications have largely fallen into disuse (Neill 1987; but see Stiles 1985; Altshuler 2006), leaving almost all research focused on territoriality and traplining.

Before we can begin to predict the traits associated with quintessential territoriality and traplining, it is important to explore the conditions under which a hummingbird would actually employ either strategy. Foraging behavior is often rooted in the energetic, competitive, and risk landscapes, and hummingbirds show remarkable plasticity, altering their foraging behavior and defense tactics depending on the context (Kodric-Brown and Brown 1978; Hixon et al. 1983; Justino et al. 2012). A territory must yield enough nectar (e.g., volumes, concentrations, and ultimately net energy gain) to support at least the costs of foraging, defense, and (when applicable) energetically-expensive mating and displays (Brown 1964; Stiles 1971; Wolf and Hainsworth 1971; Linhart 1973; Ewald and Carpenter 1978; Powers 1987). Meanwhile, the resources on a trapline must reach an energetic threshold to support breeding activities (when applicable) and be worth revisiting after traveling long distances, but not defending—which will depend on the size and energy expenditure of the individual in question (Feinsinger and Chaplin 1975; Stiles 1978; Kodric-Brown and Brown 1978; Tiebout 1991; Gass and Roberts 1992;

Garrison and Gass 1999). Thus, the spatial and temporal distribution of resources heavily influence foraging strategies and competition within an avian community (Maurer 1984).

As floral density and productivity increase, territorialists reduce the size of their territories, within which they spend more time, feed more often, and engage in increasingly energetically-expensive defense maneuvers (Kodric-Brown and Brown 1978; Ewald and Carpenter 1978; Hixon et al. 1983; Carpenter 1987; Justino et al. 2012; Lanna et al. 2017). Yet floral preference also plays a role in defense: as different plants bloom, the dominance hierarchy of a given assemblage shifts, suggesting that birds choose which resources to defend based on their reward qualities (Márquez-Luna et al. 2019). On the other hand, some individuals may abandon territoriality entirely when facing either highly lucrative territories, which demand a greater number of successful battles due to intense competition (Carpenter 1987), or areas without sufficient nectar stores to support defense (Cotton 1998b). When confronted with experimental nectar robbing—in which researchers perforated and drained all defended flowers on the birds' territories—territorialists not only expanded their defended areas, but also flew farther and consumed more insects (Hazlehurst and Karubian 2018). Females and smaller hummingbirds are more likely to be displaced or to take up territory parasitism (Kodric-Brown and Brown 1978; Abrahamczyk and Kessler 2015). Due to the intense energetic demands of nesting, females are especially unlikely to hold territories over the course of the breeding season; during this period they tend to parasitize the fringes of male territories (Wolf 1975) and consume a disproportionately greater quantity of arthropods (Rico-Guevara 2008).

Research on the behavioral flexibility of traplining species has remained relatively sparse, due to the aforementioned logistical challenges of tracking small birds across long distances.

Studies of traplining and its relationship to resource availability have largely been confined to

aviary-feeder arrays (Garrison and Gass 1999), or experiments with artificial flowers (Tello-Ramos et al. 2015). However, foraging decisions made by trapliners are similar to those of territorialists. Under conditions of heightened nectar availability or concentration, traplining species will limit the distances that they forage and increase visitation rate to more profitable feeders (Garrison and Gass 1999; Lanna et al. 2017). Additionally, traplining hummingbirds appear to visit feeders more frequently when they perceive competition, as exploitative strategies entail visiting a resource before others (Garrison and Gass 1999). While these controlled studies are beneficial for their tractability, studies of free-living trapliners would greatly increase our understanding of their energetics, for hummingbirds can and will travel much longer distances than those within an aviary.

It is common for certain species or individuals to utilize both territoriality and traplining at different times (Arizmendi et al. 2020; Schuchmann et al. 2020; Taylor 2020; Weller et al. 2020; Fernández et al. 2021), flexibility likely dictated by resource availability. Species that exhibit sporadic strategies and occasional low-reward traplining are dubbed “facultative trapliners” (Feinsinger and Colwell 1978). Even florally specialized trapliners, such as the Green Hermit (*Phaethornis guy*), will occasionally defend larger clumps of flowers for transitory periods of time, if they supply enough energy (Stiles 1985). It may be more appropriate to characterize the foraging strategies of different species by season (Stiles 1985), but hummingbirds can switch their behaviors over even finer temporal scales (Thomas et al. 1986). This prevalence of flexible foraging behavior suggests that unequivocally classifying hummingbirds by a single strategy could be limiting, a challenge we must consider when establishing morphological correlates with different behaviors.

We argue that territorialists and trappliners (following the definitions in the glossary) face divergent forces of selection, yielding birds specialized for either strategy. We predict that **1**) this specialization is based around different mechanisms of managing inter- and intraspecific competitors (Maurer 1984), such that adaptations for territoriality and trapplining are molded by interference and exploitative competition, respectively (Fig. 2) (Bourlot et al. 2014).

Quintessential territorialists and trappliners can still be influenced by both forms of competition (e.g., a non-territorial individual's use of particular resources could be affected by others engaging in interference behavior), whether from conspecifics (Temeles et al. 2006) or heterospecifics (Temeles and Kress 2010; Mendiola-Islas et al. 2016). Though the extent to which these competitive contexts vary by species and assemblage remains poorly understood, to excel in one strategy requires competitive behaviors that may compromise a bird's ability to excel in another. In his model of interference and exploitation in avian communities, Maurer (1984) assumes that an individual cannot utilize resources while actively interfering with another individual's access to those resources (compatible with the concepts of stationary interference and traveling exploitation). Thus, we expect evolutionary trade-offs through morphological, kinematic, and behavioral traits (Fig. 2). Note that while we predict that these two strategies face divergent selective forces, this is not incompatible with a foraging continuum, such that individuals can and should be described based on the percent time they spend employing different strategies over a given temporal scale (e.g., season, year).

Body Size

Hummingbirds vary widely in size, a trait that affects not only competitive interactions but also associated selective pressures. While individual hummingbirds can weigh over 23g, such as in the aggressive Giant Hummingbird (*Patagona gigas*) (Heynen et al. 2020; but see Wester and Claßen-Bockhoff 2006 for reports of nonagonistic behavior), males of the Bee Hummingbird (*Mellisuga helenae*) defend territories and can weigh as little as 2g (Vázquez 2009; Jiménez et al. 2014). Body size has been consistently linked with interspecific dominance hierarchies among hummingbirds, with larger size conferring greater defense capacity through displacement of smaller birds (Lyon 1976; Pimm et al. 1985; Carpenter et al. 1993). The largest and most frequently aggressive hummingbirds often reside at the top of their hierarchies (Antunes 2003; Abrahamczyk and Kessler 2015; Lanna et al. 2017; López-Segoviano et al. 2018; Márquez-Luna et al. 2019). This is even demonstrated within parasitic interactions—the larger an intruder is, the less likely the territory holder is to attack, suggesting that hummingbirds must weigh the cost of defense (e.g., potential injury) against the benefit of exclusive access to resources (Dearborn 1998). It appears that all dominant species may meet a minimum mass threshold (4g) and scale up from there (Bribiesca et al. 2019). Excluding hermits, only the ‘bees’ (long-distance migrants) consistently fall below this threshold (Rodríguez-Flores et al. 2019). We predict that **2**) territorialists will face selection for large body size (Fig. 2) (Feinsinger and Colwell 1978; Altshuler 2006).

It is important to recognize that the relationship between body size and territoriality is context-dependent. Many small species are territorial (e.g. the Rufous Hummingbird; average

mass ~3.3g) (Cornell 2017; Healy and Calder 2020), and species that are both aggressive *and* abundant (e.g., brilliants and mangos) appear to fall within an intermediate size range (Bribiesca et al. 2019). Furthermore, latitudinal migrants tend to be smaller than—and subordinate to—their residential counterparts, and are more likely to be non-territorial (Rodríguez-Flores and Arriaga 2016). This finding is driven by overwintering ‘bees’ (Bribiesca et al. 2019), which display vastly different hierarchical positions on their breeding grounds (Márquez-Luna et al. 2019). For a species to excel in migration, they may need to compromise competitive ability, or vice versa (Rodríguez-Flores and Arriaga 2016; Bribiesca et al. 2019).

Trapliners may face selective pressure for commuting rather than combat, and due to their noncontinuous access to each plant in their foraging sequences, their body size is likely more constrained by the amount of energy the flowers can provide (Hainsworth and Wolf 1972b). Low-reward trapliners, adhering to foraging circuits across smaller, more generalist flowers, may face selection for smaller body size (Feinsinger and Colwell 1978). While this possibly reduces competition, agonistic interactions, and their metabolic needs (Feinsinger and Colwell 1978), smaller hummingbirds compete with insects over plants containing low volumes of concentrated nectar (Dalsgaard et al. 2008, 2009). Hermits, ranging in size from less than 3g (Hinkelmann and Boesman 2020) to over 10g (Stiles 2004; Betancourth-Cundar et al. 2020), are generally considered high-reward trapliners (Linhart 1973; Stiles 1975) and have been found to hide even when in the presence of comparatively smaller (shorter and/or lighter) species, so long as those birds are dominant (Lanna et al. 2017). Plants that are functionally specialized for pollination by specific hummingbirds are characterized by longer corollas, greater nectar stores, and wider spacing, and are associated with larger hummingbirds (Dalsgaard et al. 2008, 2009) that tend to trapline across longer distances (Hadley et al. 2018). We predict that **3**) this apparent

divergence in size between high- and low-reward trapliners will be maintained across a wider selection of species (Fig. 2) (Feinsinger and Colwell 1978).

Large hummingbirds, regardless of foraging strategy, must consume more total nectar than smaller birds (Lanna et al. 2017). Larger hummingbirds tend to feed on larger flowers with greater nectar stores (Snow and Snow 1972), have longer foraging bouts, and probe more flowers per bout than smaller birds (Mendonça and Anjos 2006). On the other hand, previous work on the scaling relationship between energetics and body size has shown that, compared to smaller species, larger ones tend to have both higher mechanochemical efficiency while hovering (i.e. are better able to convert chemical energy to mechanical energy needed to sustain flight) (Groom et al. 2018) and similar mass-specific daily energy expenditure (Shankar, Powers et al. 2020). Thus, larger territorialists and trapliners (Hadley et al. 2018; López-Segoviano et al. 2018) may face energetic trade-offs regarding their size, as well as similar caloric demands to sustain their weight in flight. However, these different strategies, and the amount of activity associated with each, presumably affect a hummingbird's ability to meet such energetic requirements (Powers et al. 2003). Future research on the relationship between body size and the energetics of various foraging strategies is warranted.

Flight models and Aerodynamics

When focusing on natural selection as it pertains to foraging behavior, it is essential to consider aerodynamics and power requirements, as they affect a given hummingbird's ability to commute and/or succeed in combat. Early **wing disc loading (WDL)**, (see Glossary) models were assumed to accurately predict a bird's respective hovering costs, and therefore act as proxies for

flight performance (Hainsworth and Wolf 1972a; Weis-Fogh 1972; Epting and Casey 1973; Ellington 1984b). These models thus offered a new basis for foraging comparisons, with hummingbirds expected to evolve a relative wing size/shape that would reduce their energy use (Feinsinger and Chaplin 1975). Hence, a territorialist would exhibit high WDL (relatively shorter wings with respect to mass), which would demand more energy to hover but might confer greater agility for aggressive encounters; a trapliner was expected to exhibit low WDL (relatively longer wings) to increase foraging efficiency (Feinsinger and Chaplin 1975; Feinsinger and Colwell 1978; Epting 1980).

When applied across hummingbird assemblages, however, WDL proves overall to be an insignificant predictor of hovering costs. Rather than have high WDL (shorter wings), successful competitors actually appear to have significantly lower WDL (longer wings) than subordinates (Altshuler, Stiles, et al. 2004). Larger hummingbirds, generally more dominant (e.g., Abrahamczyk and Kessler 2015; Lanna et al. 2017; Bribiesca et al. 2019), have relatively greater burst power (see below) and relatively larger wing areas (lower **wing loading**, see Glossary) which may contribute to heightened territorial performance due to enhanced **maneuverability** (see Glossary) (Skandalis et al. 2017; Dakin et al. 2018). Due to their commuting flights, traplining hummingbirds may face selection for smaller wings (but see Stiles 2008), which require faster speeds for comparable lift generation (Norberg 1995). Further research is needed to disentangle the effects of relative wing size and shape on commuting. Surprisingly, females and juvenile males (which are generally submissive) of the ‘bee’ clade tend to have relatively longer (lower WDL) and broader wings than those of adult males, although this appears to be more related to male mating displays than competitive dominance (Stiles 1995; Stiles et al. 2005). Aside from this, hummingbirds with relatively larger wings and greater capacity to produce

power will maneuver less predictably (due to greater acceleration and more rapid/complex turns), but also while flying more slowly, suggesting a trade-off between entropy and velocity (Berberi et al. 2020). We predict that **4**) territorialists will display greater maneuverability at the expense of higher forward flight costs; in contrast, trapliners may sacrifice maneuverability in favor of lower forward flight costs to optimize their long-distance commutes (Fig. 2) (Rico-Guevara et al. 2019). This is similar to the predictions made by Feinsinger and Chaplin (1975) yet emphasizes the evolution of larger wings for turning and acceleration rather than for reducing hovering costs (which may be less in territorialists), and makes use of a recently established operational definition of maneuverability (Dakin et al. 2018). We propose that the morphological foundations for maneuverability and flight energetics are related to wing loading rather than wing disc loading, a shift that has significant methodological ramifications (measuring tracings/collections of extended wings as opposed to the chord of closed/folded wings, respectively) (Stiles et al. 2005).

Burst power (BP, see Glossary), or the maximum power output that can be elicited by a hummingbird, has been found to be an important contributor to flight performance (Chai et al. 1997; Altshuler, Dudley, and McGuire 2004; Altshuler et al. 2010; Segre et al. 2015) and a more reliable metric than WDL models (Altshuler and Dudley 2002; Altshuler, Stiles, et al. 2004; Stiles et al. 2005; Altshuler 2006). BP has been significantly correlated with interspecific defense, with territorialists producing more BP than non-territorialists (a large category which includes trapliners, generalists, marauders, and filchers) (Altshuler 2006; but see Araya-Salas et al. 2018 on intraspecific interactions). BP is one of the most important predictors of maneuverability, more so than wing morphological traits (Segre et al. 2015; Dakin et al. 2018). Birds with greater BP exhibit greater translational velocity and horizontal accelerations, faster

rotations, and more efficient complex turns (Segre et al. 2015, 2016; Dakin et al. 2018). During agonistic interactions, which are generally short but intense chases and/or fights, a territorialist is likely constrained by their maximum capacity for muscle strain and power (Hedrick et al. 2012). In an unrestricted natural chase, a hummingbird is more likely to reach its lab-based maximum flight force and kinematic power than its maximum flight speed (Sholtis et al. 2015). We predict that **5)** across species within a complex assemblage, territorialists will consistently produce more burst power than trapliners (Fig. 2). It should be noted that studies on load-lifting and flight performance are focused on males (e.g., Segre et al. 2015; Dakin et al. 2018); corresponding data on females are lacking and needed.

The extent to which a hummingbird can produce BP may depend on the size of the flight musculature (Altshuler and Dudley 2002). If territorialists are indeed facing selection for maximal power to aid in aerial combat and active interference, this may take the form of selection for relatively larger flight muscles (pectoralis and supracoracoideus). We predict that **6)** controlling for body size, territorialists will have larger flight muscles than trapliners (Fig. 2), which do not engage in chases as frequently (Lanna et al. 2017). Energetic costs can constrain muscle size, as basal metabolic rate (a measurement of energetic costs of maintenance) is strongly correlated with skeletal muscle size (Weber and Piersma 1996; Chappell et al. 1999; Petit et al. 2014; Vezina et al. 2017). Given that hummingbirds possess relatively large flight muscle mass (up to 33% of total body mass) (Altshuler and Dudley 2002), we predict that **7)** traplining species may forgo larger muscles to reduce basal metabolic rate (BMR) more than territorialists (Fig. 2).

Future Directions and Concluding Remarks

While the predictions outlined here may seem incompatible with the concept of a foraging continuum, we argue that an individual bird, and much less a given sex/species, is not limited to one strategy or the other. Hummingbirds adjust their foraging behavior regularly, whether due to extrinsic factors like floral availability or presence of competitors (Ewald and Carpenter 1978; Powers et al. 2003; Justino et al. 2012; Abrahamczyk and Kessler 2015; Márquez-Luna et al. 2019), or intrinsic factors such as energetics, breeding season, or migratory patterns (Wolf 1975; Rodríguez-Flores and Arriaga 2016; Bribiesca et al. 2019; Márquez-Luna et al. 2019). This behavioral plasticity, as well as the existence of intermediate traits and foragers (Abrahamczyk and Kessler 2015; Arizmendi et al. 2020; Puga-Caballero et al. 2020; Schuchmann et al. 2020; Weller et al. 2020), provide essential context for understanding the conditions under which a hummingbird might employ territoriality versus traplining. We believe that the process of describing these birds should rely on the percent time (across a season or year) that an individual engages in various strategies, but this has yet to be quantified. Furthermore, very little work has been done to explore alternative foraging strategies, and the majority of research has centered around the much more accessible territorialists. This has greatly affected our ability to draw accurate conclusions regarding hummingbirds' energetics and life histories. Our understanding of this continuum could greatly benefit from further research on the additional strategies proposed by Feinsinger and Colwell (1978).

Along with the flexibility of hummingbird behavior, we highlight the morphological traits that impose hard limits to what can be accomplished via modification of kinematics—which, in turn, is limited by myology and physiology. We have established testable predictions regarding the behavioral, locomotor, and energetic facets of territoriality and traplining (Fig. 2).

By focusing on these predictions, future research could greatly enhance our understanding of the natural selection forces at play on a highly specialized, energetically constrained group of birds. Such research would provide a basis for examining potentially conflicting selective forces to maximize both energetic efficiency and ability to compete for resources, and ways in which to systematically study presumed trade-offs, on a broad, family-level scale. Subsequent studies should focus on traits that display inextricable links between sexual and natural selection—such as bill morphology, coloration, and vocalizations—and their implications for foraging strategies. Testing the predictions outlined here, starting with the suggested methods in Figure 2, is a step closer to understanding such selective processes.

Recent studies of hummingbird flight performance have employed high-speed cameras (Sholtis et al. 2015), X-ray videography with micro-computed tomography (Hedrick et al. 2012), and automated tracking systems (Segre et al. 2015, 2016; Dakin et al. 2018). All of these tools have improved our ability to build upon earlier studies, and often answer questions that cannot be addressed without them. Future work could leverage these technological advances to explore the relationship between wing morphology and flight performance as they pertain to foraging strategies. Despite additional methodological innovations (e.g., doubly-labeled water, radio-tags, open-flow respirometry systems) (Powers et al. 2003; Groom et al. 2018; Hazlehurst and Karubian 2018; Shankar et al. 2019; Shankar, Schroeder et al. 2020), our current understanding of how the energetic costs of locomotion vary across foraging strategies is poor, especially in the context of wing morphology and the relative proportion of time spent hovering, commuting, and/or chasing competitors. Tracking technologies (Hadley and Betts 2009; Hazlehurst and Karubian 2018), combined with advanced camera/video traps (Rico-Guevara and Mickley 2017; Tinoco et al. 2017; Sonne et al. 2019) and motion-detection software (Weinstein 2015), enable

assessing trapliner movements and energetics in much greater detail, and across larger scales, than ever before.

Using the wealth of research on foraging constraints and behavior of hummingbirds, we have the ability to clarify the operational definitions of territoriality and traplining from a quantitative perspective. Future work will aim to examine, describe, and formulate tests for divergent strategies that could be implemented on free-living hummingbirds, in order to explore their foraging spectrum. This research may resolve inconsistencies, both conceptually and in the field, and formulate suggestions that could be extrapolated to the classifications of other nectarivores. Despite a plethora of studies, hummingbird foraging still remains enigmatic, with many lingering questions that we now have the technological capabilities to resolve.

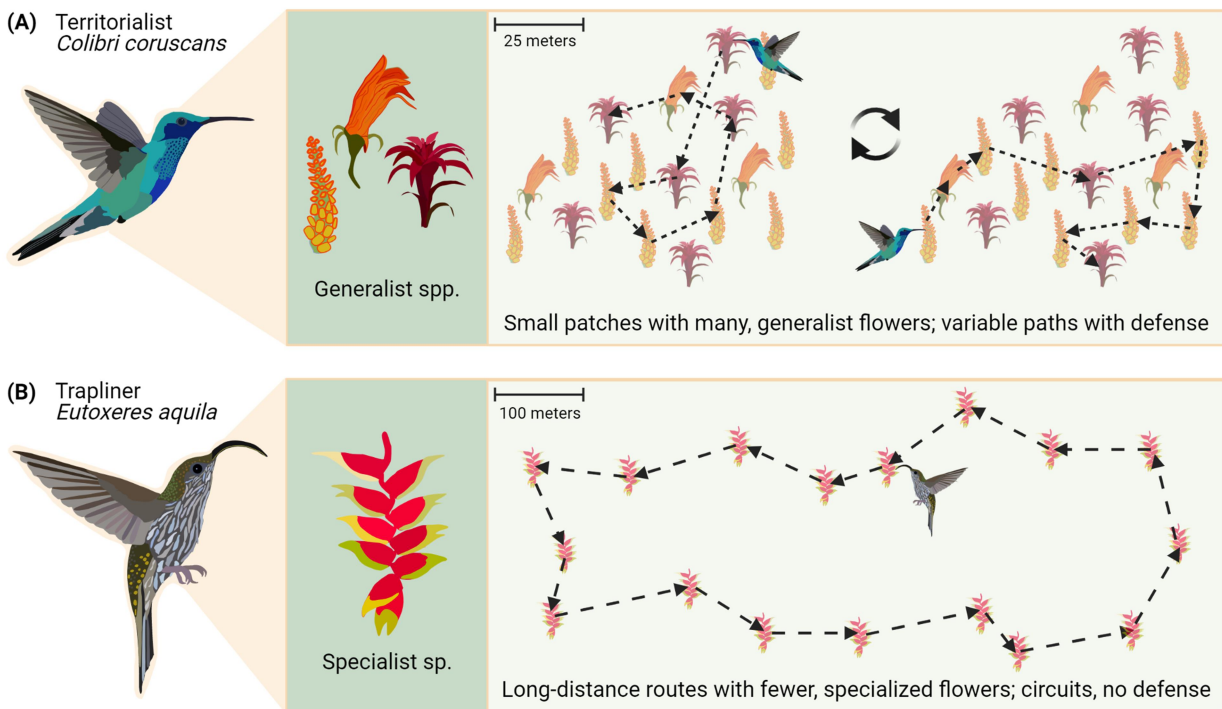
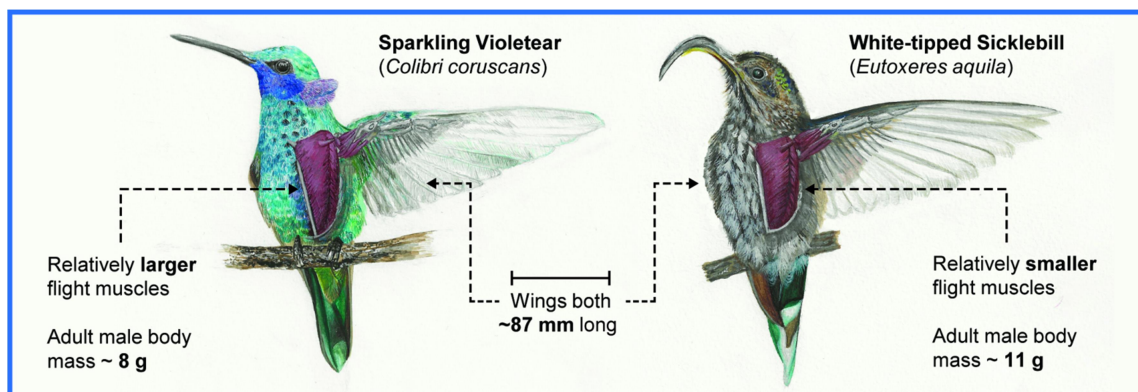


Figure 1. Traditional understanding of major hummingbird foraging strategies. (A) Quintessential territorialist represented by the Sparkling Violetear (*Colibri coruscans*), which feeds from numerous generalist plants, including *Elleanthus* (left), *Siphocampylus* (middle), and *Guzmania* (right). **(B)** Quintessential trapliner represented by the White-tipped Sicklebill (*Eutoxeres aquila*), which is a nearly obligate mutualist with plants like *Heliconia*. Scale bars included to show spatial scale of visited flowers. Figure created with BioRender.com.



Trait (Prediction #)	Territorialist	Trapliner	Suggested Methods
Major competitive behavior (1)	Interference (Feinsinger and Chaplin 1975; Feinsinger, Colwell, et al. 1979)	Exploitation (Feinsinger and Chaplin 1975; Feinsinger, Colwell, et al. 1979)	Behavioral and advanced tracking (Hazlehurst and Karubian 2018), nectar competition estimations (Gill and Wolf 1979)
Body size (2-3)	Large size confers competitive edge (Abrahamczyk and Kessler 2015; Bribiesca et al. 2019)	Large if florally specialized (Hadley et al. 2018), otherwise small (Feinsinger and Colwell 1978)	Phylogenetically controlled analyses of morphometrics and literature surveys (e.g., PCA; Labocha and Hayes 2012)
Burst power (5)*	Greater (Altshuler 2006)	Lower (Altshuler 2006)	Asymptotic load lifting (Altshuler et al. 2010; Segre et al. 2015)
Maneuverability (4)*	Greater	Lower	3D flight tracking, wing loading measurements (Sholtis et al. 2015; Dakin et al. 2018)
Flight muscle mass (6)*	Greater	Lower	Targeted dissections (Altshuler and Dudley 2002) coupled with basal metabolic rate studies
Basal metabolic rate (7)*	Greater	Lower	Closed-chamber respirometry (Fernández et al. 2011) coupled with flight muscle mass studies

*Relative to body size

Figure 2. Predicted behavioral, biomechanical, and morphofunctional associations with territoriality and traplining. Quintessential territorialist (left) represented by Sparkling Violetear; trapliner (right) represented by White-tipped Sicklebill. See embedded sources for more information. Mass data acquired from Hainsworth 1977; Betancourth-Cundar et al. 2020.

Literature Cited

- Abrahamczyk S, Kessler M. 2015. Morphological and behavioural adaptations to feed on nectar: how feeding ecology determines the diversity and composition of hummingbird assemblages. *J Ornithol* 156:333–47.
- Altshuler DL. 2006. Flight Performance and Competitive Displacement of Hummingbirds across Elevational Gradients. *The American Naturalist* 167:216–29.
- Altshuler DL, Dudley R. 2002. The ecological and evolutionary interface of hummingbird flight physiology. *Journal of Experimental Biology* 205:2325–36.
- Altshuler DL, Dudley R, Ellington CP. 2004. Aerodynamic forces of revolving hummingbird wings and wing models. *Journal of Zoology* 264:327–32.
- Altshuler DL, Dudley R, Heredia SM, McGuire JA. 2010. Allometry of hummingbird lifting performance. *Journal of Experimental Biology* 213:725–34.
- Altshuler DL, Dudley R, McGuire JA. 2004. Resolution of a paradox: Hummingbird flight at high elevation does not come without a cost. *PNAS* 101:17731–36.
- Altshuler DL, Stiles FG, Dudley R. 2004. Of Hummingbirds and Helicopters: Hovering Costs, Competitive Ability, and Foraging Strategies. *The American Naturalist* 163:16–25.
- Antunes AZ [UNESP.] 2003. Partilha de néctar de *Eucalyptus* spp., territorialidade e hierarquia de dominância em beija-flores (Aves: Trochilidae) no sudeste do Brasil. *Eucalyptus nectar resource partitioning, territoriality and dominance hierarchy in hummingbirds (Aves: Trochilidae) in southeastern Brazil* 39–44.
- Araya-Salas M, Gonzalez-Gomez P, Wojczulanis-Jakubas K, López V, Wright TF. 2018. Spatial memory is as important as weapon and body size for territorial ownership in a lekking

- hummingbird. Scientific Reports 8:2001.
- Arizmendi M del C, Rodríguez-Flores CI, Soberanes-González CA, Schulenberg TS. 2020. Plain-capped Starthroat (*Heliomaster constantii*). Birds of the World.
- Berberi I, Segre PS, Altshuler DL, Dakin R. 2020. Unpredictable hummingbirds: Flight path entropy is constrained by speed and wing loading. bioRxiv 2020.08.11.246926.
- Betancourth-Cundar M, Beltran-Arevalo B-A, Torres-Sánchez P. 2020. White-tipped Sicklebill (*Eutoxeres aquila*). Birds of the World.
- Betts MG, Hadley AS, Kress WJ. 2015. Pollinator recognition by a keystone tropical plant. PNAS 112:3433–38.
- Birkhead T. 2008. The wisdom of birds: an illustrated history of ornithology. Walker Books. 205-238.
- Bribiesca R, Herrera-Alsina L, Ruiz-Sanchez E, Sánchez-González LA, Schondube JE. 2019. Body mass as a supertrait linked to abundance and behavioral dominance in hummingbirds: A phylogenetic approach. Ecology and Evolution 9:1623–37.
- Brown JL. 1964. The Evolution of Diversity in Avian Territorial Systems. The Wilson Bulletin 76:160–69.
- Carpenter FL. 1987. Food Abundance and Territoriality: To Defend or Not to Defend? Am Zool 27:387–99.
- Carpenter FL, Hixon MA, Russell RW, Paton DC, Temeles EJ. 1993. Interference Asymmetries among Age-Sex Classes of Rufous Hummingbirds during Migratory Stopovers. Behavioral Ecology and Sociobiology 33:297–304.
- Chai P, Chen JS, Dudley R. 1997. Transient hovering performance of hummingbirds under conditions of maximal loading. Journal of Experimental Biology 200:921–29.

- Chai P, Millard D. 1997. Flight and size constraints: hovering performance of large hummingbirds under maximal loading. *Journal of Experimental Biology* 200:2757–63.
- Chappell MA, Bech C, Buttemer WA. 1999. The relationship of central and peripheral organ masses to aerobic performance variation in house sparrows. *Journal of Experimental Biology* 202:2269–79.
- Cornell. 2017. Rufous Hummingbird Overview, All About Birds, Cornell Lab of Ornithology. (https://www.allaboutbirds.org/guide/Rufous_Hummingbird/overview).
- Cotton PA. 1998a. Coevolution in an Amazonian hummingbird-plant community. *Ibis* 140:639–46.
- Cotton PA. 1998b. Temporal partitioning of a floral resource by territorial hummingbirds. *Ibis* 140:647–53.
- Dakin R, Segre PS, Altshuler DL. 2020. Individual variation and the biomechanics of maneuvering flight in hummingbirds. *J Exp Biol* 223:jeb161828.
- Dakin R, Segre PS, Straw AD, Altshuler DL. 2018. Morphology, muscle capacity, skill, and maneuvering ability in hummingbirds. *Science* 359:653–57.
- Dalsgaard B, González AMM, Olesen JM, Timmermann A, Andersen LH, Ollerton J. 2008. Pollination networks and functional specialization: a test using Lesser Antillean plant–hummingbird assemblages. *Oikos* 117:789–93.
- Dalsgaard B, Martín González AM, Olesen JM, Ollerton J, Timmermann A, Andersen LH, Tossas AG. 2009. Plant-hummingbird interactions in the West Indies: floral specialisation gradients associated with environment and hummingbird size. *Oecologia* 159:757–66.
- Dearborn DC. 1998. Interspecific Territoriality by a Rufous-Tailed Hummingbird (*Amazilia*

- tzacatl*): Effects of Intruder Size and Resource Value. *Biotropica* 30:306–13.
- Deygout C, Gault A, Sarrazin F, Bessa-Gomes C. 2009. Modeling the impact of feeding stations on vulture scavenging service efficiency. *Ecological Modelling* 220:1826–35.
- Drury JP, Cowen MC, Grether GF. 2020. Competition and hybridization drive interspecific territoriality in birds. *Proc Natl Acad Sci USA* 117:12923–30.
- Ellington CP. 1984. The Aerodynamics of Hovering Insect Flight. V. A Vortex Theory. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences* 305:115–44.
- Epting RJ. 1980. Functional Dependence of the Power for Hovering on Wing Disc Loading in Hummingbirds. *Physiological Zoology* 53:347–57.
- Epting RJ, Casey TM. 1973. Power Output and Wing Disc Loading in Hovering Hummingbirds. *The American Naturalist* 107:761–65.
- Evens J, Harper C. 2020. Lethal Intraspecific Behavior by Anna's Hummingbird. *nwnt* 101:221–22.
- Ewald PW, Carpenter FL. 1978. Territorial Responses to Energy Manipulations in the Anna Hummingbird. *Oecologia* 31:277–92.
- Feinsinger P. 1976. Organization of a Tropical Guild of Nectarivorous Birds. *Ecological Monographs* 46:257–91.
- Feinsinger P, Chaplin SB. 1975. On the Relationship between Wing Disc Loading and Foraging Strategy in Hummingbirds. *The American Naturalist* 109:217–24.
- Feinsinger P, Colwell RK. 1978. Community Organization Among Neotropical Nectar-Feeding Birds. *Integr Comp Biol* 18:779–95.
- Feinsinger P, Colwell RK, Terborgh J, Chaplin SB. 1979. Elevation and the Morphology, Flight

- Energetics, and Foraging Ecology of Tropical Hummingbirds. *The American Naturalist* 113:481–97.
- Fernández CM, Luther D, Heynen I, Boesman PFD, Kirwan GM. 2021. Great Sapphirewing (*Pterophanes cyanopterus*). *Birds of the World*.
- Fernández MJ, Dudley R, Bozinovic F. 2011. Comparative Energetics of the Giant Hummingbird (*Patagona gigas*). *Physiological and Biochemical Zoology* 84:333–40.
- Freeman RB. 1968. Charles Darwin on the Routes of Male Humble Bees. *C R* 14.
- Fretwell SD, Calver JS. 1969. On territorial behavior and other factors influencing habitat distribution in birds: II. Sex ratio variation in the Dickcissel (*Spiza americana* Gmel). *Acta Biotheoretica* 19:37–44.
- Garber PA. 1988. Foraging Decisions During Nectar Feeding by Tamarin Monkeys (*Saguinus mystax* and *Saguinus fuscicollis*, Callitrichidae, Primates) in Amazonian Peru. *Biotropica* 20:100–106.
- Garrison JSE. 1995. Traplining foraging behavior in a tropical hummingbird species *Phaethornis superciliosus*.
- Garrison JSE, Gass CL. 1999. Response of a traplining hummingbird to changes in nectar availability. *Behavioral Ecology* 10:714–25.
- Gass CL, Garrison JSE. 1999. Energy regulation by traplining hummingbirds. *Functional Ecology* 13:483–92.
- Gass CL, Roberts WM. 1992. The Problem of Temporal Scale in Optimization: Three Contrasting Views of Hummingbird Visits to Flowers. *The American Naturalist* 140:829–53.
- Gilbert LE, Singer MC. 1975. Butterfly Ecology. *Annu Rev Ecol Syst* 6:365–95.

- Gill FB. 1988. Trapline Foraging by Hermit Hummingbirds: Competition for an Undefended, Renewable Resource. *Ecology* 69:1933–42.
- Gill FB, Wolf LL. 1979. Nectar Loss by Golden-Winged Sunbirds to Competitors. *The Auk* 96:448–61.
- Gould E. 1978. Foraging Behavior of Malaysian Nectar-Feeding Bats. *Biotropica* 10:184–93.
- Greenberg R, Gradwohl J. 1986. Constant density and stable territoriality in some tropical insectivorous birds. *Oecologia* 69:618–25.
- Groom DJE, Toledo MCB, Powers DR, Tobalske BW, Welch KC. 2018. Integrating morphology and kinematics in the scaling of hummingbird hovering metabolic rate and efficiency. *Proceedings of the Royal Society B: Biological Sciences* 285:20172011.
- Hadley AS, Betts MG. 2009. Tropical deforestation alters hummingbird movement patterns. *Biology Letters* rsbl.2008.0691.
- Hadley AS, Frey SJK, Robinson WD, Betts MG. 2018. Forest fragmentation and loss reduce richness, availability, and specialization in tropical hummingbird communities. *Biotropica* 50:74–83.
- Hainsworth FR. 1977. Foraging Efficiency and Parental Care in *Colibri coruscans*. *The Condor* 79:69–75.
- Hainsworth FR, Wolf LL. 1972a. Power for Hovering Flight in Relation to Body Size in Hummingbirds. *The American Naturalist* 106:589–96.
- Hainsworth FR, Wolf LL. 1972b. Energetics of nectar extraction in a small, high altitude, tropical hummingbird, *Selasphorus flammula*. *J Comp Physiol* 80:377–87.
- Hassell MP, Southwood TRE. 1978. Foraging Strategies of Insects. *Annual Review of Ecology and Systematics* 9:75–98.

- Hazlehurst JA, Karubian JO. 2018. Impacts of nectar robbing on the foraging ecology of a territorial hummingbird. *Behavioural Processes* 149:27–34.
- Healy S, Calder WA. 2020. Rufous Hummingbird (*Selasphorus rufus*). *Birds of the World*.
- Hedrick TL, Tobalske BW, Ros IG, Warrick DR, Biewener AA. 2012. Morphological and kinematic basis of the hummingbird flight stroke: scaling of flight muscle transmission ratio. *Proc R Soc B* 279:1986–92.
- Heynen I, Boesman PFD, Kirwan GM. 2020. Giant Hummingbird (*Patagona gigas*). *Birds of the World*.
- Hinkelmann C, Boesman PFD. 2020. White-browed Hermit (*Phaethornis stuarti*). *Birds of the World*.
- Hixon MA, Carpenter FL, Paton DC. 1983. Territory Area, Flower Density, and Time Budgeting in Hummingbirds: An Experimental and Theoretical Analysis. *The American Naturalist* 122:366–91.
- Janzen DH. 1971. Euglossine Bees as Long-Distance Pollinators of Tropical Plants. *Science* 171:203–5.
- Jiménez A, García-Lau I, González A, Mugica L, Acosta M. 2014. Masa corporal de 183 especies de aves cubanas / Body mass of 183 species of Cuban birds. *Revista Cubana de Ciencias Biológicas* 3:22–42.
- Justino DG, Maruyama PK, Oliveira PE. 2012. Floral resource availability and hummingbird territorial behaviour on a Neotropical savanna shrub. *J Ornithol* 153:189–97.
- Kodric-Brown A, Brown JH. 1978. Influence of Economics, Interspecific Competition, and Sexual Dimorphism on Territoriality of Migrant Rufous Hummingbirds. *Ecology* 59:285–96.

Labocha MK, Hayes JP. 2012. Morphometric indices of body condition in birds: a review. *J Ornithol* 22.

Lanna LL, Azevedo CS de, Claudino RM, Oliveira R, Antonini Y. 2017. Feeding behavior by hummingbirds (Aves: Trochilidae) in artificial food patches in an Atlantic Forest remnant in southeastern Brazil. *Zoologia (Curitiba)* 34.

Le Bourlot V, Tully T, Claessen D. 2014. Interference versus Exploitative Competition in the Regulation of Size-Structured Populations. *The American Naturalist* 184:609–23.

Lemke TO. 1984. Foraging Ecology of the Long-Nosed Bat, *Glossophaga Soricina*, With Respect to Resource Availability. *Ecology* 65:538–48.

Lihoreau M, Chittka L, Raine NE. 2011. Trade-off between travel distance and prioritization of high-reward sites in traplining bumblebees. *Functional Ecology* 25:1284–92.

Lihoreau M, Raine NE, Reynolds AM, Stelzer RJ, Lim KS, Smith AD, Osborne JL, Chittka L. 2013. Unravelling the mechanisms of trapline foraging in bees. *Commun Integr Biol* 6.

Linhart YB. 1973. Ecological and Behavioral Determinants of Pollen Dispersal in Hummingbird- Pollinated *Heliconia*. *The American Naturalist* 107:511–23.

López-Segoviano G, Bribiesca R, Arizmendi MDC. 2018. The role of size and dominance in the feeding behaviour of coexisting hummingbirds. *Ibis* 160:283–92.

Lyon DL. 1976. A Montane Hummingbird Territorial System in Oaxaca, Mexico. *The Wilson Bulletin* 88:280–99.

Lyon DL, Crandall J, McKone M. 1977. A Test of the Adaptiveness of Interspecific Territoriality in the Blue-Throated Hummingbird. *The Auk* 94:448–54.

Maher CR, Lott DF. 1995. Definitions of territoriality used in the study of variation in vertebrate spacing systems. *Animal Behaviour* 49:1581–97.

- Márquez-Luna U, Lara C, Corcuera P, Valverde PL. 2019. Factors affecting the dominance hierarchy dynamics in a hummingbird assemblage. *Current Zoology* 65:261–68.
- Maurer BA. 1984. Interference and Exploitation in Bird Communities. *The Wilson Bulletin* 96:380–95.
- McGuire JA, Witt CC, Remsen JV, Corl A, Rabosky DL, Altshuler DL, Dudley R. 2014. Molecular Phylogenetics and the Diversification of Hummingbirds. *Current Biology* 24:910–16.
- Mendiola-Islas V, Lara C, Corcuera P, Valverde PL. 2016. Residency in white-eared hummingbirds (*Hylocharis leucotis*) and its effect in territorial contest resolution. *PeerJ* 4:e2588.
- Mendonça LB, Anjos L dos. 2006. Flower morphology, nectar features, and hummingbird visitation to *Palicourea crocea* (Rubiaceae) in the Upper Paraná River floodplain, Brazil. *Anais da Academia Brasileira de Ciências* 78:45–57.
- Montgomerie RD, Redsell CA. 1980. A Nesting Hummingbird Feeding Solely on Arthropods. *The Condor* 82:463.
- Neill DA. 1987. Trapliners in the Trees: Hummingbird Pollination of *Erythrina* Sect. *Erythrina* (Leguminosae: Papilionoideae). *Annals of the Missouri Botanical Garden* 74:27–41.
- Nice MM. 1941. The Role of Territory in Bird Life. *The American Midland Naturalist* 26:441–87.
- Norberg UM. 1995. How a Long Tail and Changes in Mass and Wing Shape Affect the Cost for Flight in Animals. *Functional Ecology* 9:48–54.
- Ohashi K, Thomson JD. 2009. Trapline foraging by pollinators: its ontogeny, economics and possible consequences for plants. *Ann Bot* 103:1365–78.

- Ohashi K, Thomson JD, D'Souza D. 2007. Trapline foraging by bumble bees: IV. Optimization of route geometry in the absence of competition. *Behav Ecol* 18:1–11.
- Petit M, Vézina F. 2014. Phenotype manipulations confirm the role of pectoral muscles and haematocrit in avian maximal thermogenic capacity. *The Journal of experimental biology* 217:824–30.
- Pimm SL, Rosenzweig ML, Mitchell W. 1985. Competition and Food Selection: Field Tests of a Theory. *Ecology* 66:798–807.
- Powers DR. 1987. Effects of Variation in Food Quality on the Breeding Territoriality of the Male Anna's Hummingbird. *The Condor* 89:103–11.
- Powers DR, Brown AR, Van Hook JA. 2003. Influence of Normal Daytime Fat Deposition on Laboratory Measurements of Torpor Use in Territorial versus Nonterritorial Hummingbirds. *Physiological and Biochemical Zoology* 76:389–97.
- Powers DR, McKee T. 1994. The Effect of Food Availability on Time and Energy Expenditures of Territorial and Non-Territorial Hummingbirds. *The Condor* 96:1064–75.
- Puga-Caballero A, Arizmendi M del C, Sánchez-González LA. 2020. Phylogenetic and phenotypic filtering in hummingbirds from urban environments in Central Mexico. *Evol Ecol* 34:525–41.
- Rico-Guevara A. 2008. Morphology and arthropod foraging by high Andean hummingbirds. *Colombian Ornithology* 7:43-58.
- Rico-Guevara A, Mickle J. 2017. Bring your own camera to the trap: An inexpensive, versatile, and portable triggering system tested on wild hummingbirds. *Ecology and Evolution* 7:4592–98.
- Rico-Guevara A, Rubega MA, Hurme KJ, Dudley R. 2019. Shifting Paradigms in the Mechanics

of Nectar Extraction and Hummingbird Bill Morphology. Integrative Organismal Biology 1.

Rodríguez-Flores CI, Arriaga MCA. 2016. The dynamics of hummingbird dominance and foraging strategies during the winter season in a highland community in Western Mexico. Journal of Zoology 299:262–74.

Rodríguez-Flores CI, Ornelas JF, Wethington S, Arizmendi M del C. 2019. Are hummingbirds generalists or specialists? Using network analysis to explore the mechanisms influencing their interaction with nectar resources. PLoS ONE 14:e0211855.

Sapir N, Dudley R. 2012. Backward flight in hummingbirds employs unique kinematic adjustments and entails low metabolic cost. Journal of Experimental Biology 215:3603–11.

Schuchmann K-L, Kirwan GM, Boesman PFD. 2020. Green-tailed Goldenthrout (*Polytmus theresia*). Birds of the World.

Segre PS, Dakin R, Read TJG, Straw AD, Altshuler DL. 2016. Mechanical Constraints on Flight at High Elevation Decrease Maneuvering Performance of Hummingbirds. Current Biology 26:3368–74.

Segre PS, Dakin R, Zordan VB, Dickinson MH, Straw AD, Altshuler DL. 2015. Burst muscle performance predicts the speed, acceleration, and turning performance of Anna's hummingbirds. eLife 4:e11159.

Shankar A, Graham CH, Canepa JR, Wethington SM, Powers DR. 2019. Hummingbirds budget energy flexibly in response to changing resources. Functional Ecology 33:1904–16.

Shankar A, Powers DR, Dávalos LM, Graham CH. 2020. The allometry of daily energy expenditure in hummingbirds: An energy budget approach. Journal of Animal Ecology

89:1254–61.

- Shankar A, Schroeder RJ, Wethington SM, Graham CH, Powers DR. 2020. Hummingbird torpor in context: duration, more than temperature, is the key to nighttime energy savings. *J Avian Biol* 51:jav.02305.
- Sholtis KM, Shelton RM, Hedrick TL. 2015. Field Flight Dynamics of Hummingbirds during Territory Encroachment and Defense. *PLoS ONE* 10:e0125659.
- Skandalis DA, Segre PS, Bahlman JW, Groom DJE, Jr KCW, Witt CC, McGuire JA, Dudley R, Lentink D, Altshuler DL. 2017. The biomechanical origin of extreme wing allometry in hummingbirds. *Nature Communications* 8:1047.
- Snow BK, Snow DW. 1972. Feeding Niches of Hummingbirds in a Trinidad Valley. *Journal of Animal Ecology* 41:471–85.
- Sonne J, Zanata TB, González AMM, Torres NLC, Fjeldså J, Colwell RK, Tinoco BA, Rahbek C, Dalsgaard B. 2019. The distributions of morphologically specialized hummingbirds coincide with floral trait matching across an Andean elevational gradient. *Biotropica* 51:205–18.
- Stiles FG. 1971. Time, Energy, and Territoriality of the Anna Hummingbird (*Calypte anna*). *Science* 173:818–21.
- Stiles FG. 1975. Ecology, Flowering Phenology, and Hummingbird Pollination of Some Costa Rican *Heliconia* Species. *Ecology* 56:285–301.
- Stiles FG. 1978. Ecological and Evolutionary Implications of Bird Pollination. *Am Zool* 18:715–27.
- Stiles FG. 1985. Seasonal Patterns and Coevolution in the Hummingbird-Flower Community of a Costa Rican Subtropical Forest. *Ornithological Monographs* 757–87.

- Stiles FG. 1995. Behavioral, Ecological and Morphological Correlates of Foraging for Arthropods by the Hummingbirds of a Tropical Wet Forest. *The Condor* 97:853–78.
- Stiles FG. 2004. Phylogenetic Constraints Upon Morphological and Ecological Adaptation in Hummingbirds (Trochilidae): Why Are There No Hermits in the Paramo? *Ornitologia Neotropical* 15:191–98.
- Stiles FG. 2008. Ecomorphology and phylogeny of hummingbirds: Divergence and convergence in adaptations to high elevations. *Ornitologia Neotropical* 19:511–19.
- Stiles FG, Altshuler DL, Dudley R. 2005. Wing Morphology and Flight Behavior of some North American Hummingbird Species. *The Auk* 122:872–86.
- Suarez RK, Gass CL. 2002. Hummingbird foraging and the relation between bioenergetics and behaviour. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* 133:335–43.
- Taylor J. 2020. Green-crowned Brilliant (*Heliodoxa jacula*). *Birds of the World*.
- Tello-Ramos MC, Hurly TA, Healy SD. 2015. Traplining in hummingbirds: flying short-distance sequences among several locations. *Behav Ecol* 26:812–19.
- Tello-Ramos MC, Hurly AT, Healy SD. 2019. From a sequential pattern, temporal adjustments emerge in hummingbird traplining. *Integrative Zoology* 14:182–92.
- Temeles EJ, Goldman RS, Kudla AU. 2005. Foraging and Territory Economics of Sexually Dimorphic Purple-Throated Caribs (*Eulampis Jugularis*) on Three *Heliconia* Morphs. *The Auk* 122:187–204.
- Temeles EJ, Kress WJ. 2010. Mate choice and mate competition by a tropical hummingbird at a floral resource. *Proceedings of the Royal Society B: Biological Sciences* 277:1607–13.
- Temeles EJ, Shaw KC, Kudla AU, Sander SE. 2006. Traplining by purple-throated carib

- hummingbirds: behavioral responses to competition and nectar availability. *Behavioral Ecology and Sociobiology* 61:163–72.
- Thomas CD, Lackie PM, Brisco MJ, Hepper DN. 1986. Interactions between Hummingbirds and Butterflies at a *Hamelia patens* Bush. *Biotropica* 18:161–65.
- Thomson JD, Slatkin M, Thomson BA. 1997. Trapline foraging by bumble bees: II. Definition and detection from sequence data. *Behavioral Ecology* 8:199–210.
- Tiebout HM. 1991. Daytime Energy Management by Tropical Hummingbirds: Responses to Foraging Constraint. *Ecology* 72:839–51.
- Tinoco BA, Graham CH, Aguilar JM, Schleuning M. 2017. Effects of hummingbird morphology on specialization in pollination networks vary with resource availability. *Oikos* 126:52–60.
- Tobalske BW, Warrick DR, Clark CJ, Powers DR, Hedrick TL, Hyder GA, Biewener AA. 2007. Three-dimensional kinematics of hummingbird flight. *Journal of Experimental Biology* 210:2368–82.
- Torres-Vanegas F, Hadley AS, Kormann UG, Jones FA, Betts MG, Wagner HH. 2019. The Landscape Genetic Signature of Pollination by Trapliners: Evidence From the Tropical Herb, *Heliconia tortuosa*. *Front Genet* 10.
- Vázquez AHP. 2009. Estudio preliminar de la distribución del Zunzuncito *Mellisuga helenae* (Aves: Trochilidae) en diferentes áreas de la Reserva de Biosfera Península de Guanahacabibes, Cuba. *Revista ECOVIDA* 1:216–18.
- Vézina F, Gerson AR, Guglielmo CG, Piersma T. 2017. The performing animal: causes and consequences of body remodeling and metabolic adjustments in red knots facing contrasting thermal environments. *American Journal of Physiology-Regulatory,*

- Integrative and Comparative Physiology 313:R120–31.
- Vogel ER, Kivai S, Alavi S. 2017. Foraging Strategies. In: The International Encyclopedia of Primatology American Cancer Society. p. 1–9.
- Volpe NL, Hadley AS, Robinson WD, Betts MG. 2014. Functional connectivity experiments reflect routine movement behavior of a tropical hummingbird species. *Ecological Applications* 24:2122–31.
- Warrick DR, Tobalske BW, Powers DR. 2005. Aerodynamics of the hovering hummingbird. *Nature* 435:1094–97.
- Weber TP, Piersma T. 1996. Basal Metabolic Rate and the Mass of Tissues Differing in Metabolic Scope: Migration-Related Covariation between Individual Knots *Calidris canutus*. *Journal of Avian Biology* 27:215–24.
- Weinstein BG. 2015. MotionMeerkat: integrating motion video detection and ecological monitoring. *Methods in Ecology and Evolution* 6:357–62.
- Weis-Fogh T. 1972. Energetics of Hovering Flight in Hummingbirds and in *Drosophila*. *Journal of Experimental Biology* 56:79–104.
- Weller AA, Boesman PFD, Kirwan GM. 2020. Velvet-browed Brilliant (*Heliodoxa xanthogonys*). *Birds of the World*.
- Wester P, Claßen-Bockhoff R. 2006. Hummingbird pollination in *Salvia haenkei* (Lamiaceae) lacking the typical lever mechanism. *Plant Syst Evol* 257:133–46.
- Wolf LL. 1975. Female Territoriality in the Purple-Throated Carib. *The Auk* 92:511–22.
- Wolf LL, Hainsworth FR. 1971. Time and Energy Budgets of Territorial Hummingbirds. *Ecology* 52:980–88.
- Woodsworth GC, Bell GP, Fenton MB. 1981. Observations of the echolocation, feeding

behaviour, and habitat use of *Euderma maculatum* (Chiroptera: Vespertilionidae) in southcentral British Columbia. Can J Zool 59:1099–1102.

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Glossary

Burst power (BP)

Maximum power output that can be elicited from the flight musculature; assessed by having a hummingbird take off vertically and lift increasing amounts of weight until it is unable to lift any more

Competition

Interaction between con- or heterospecifics over a limited resource (at the community level)

Exploitative competition

The actions of one individual indirectly preventing another from accessing a resource (e.g., depletion of a flower)

Interference competition

The actions of one individual directly preventing another from accessing a resource (e.g., chases)

Foraging

Searching for and obtaining food

Strategy generalist

Hummingbird that employs a flexible foraging strategy depending on resource availability

Haphazard foraging

Foraging and encountering flowers in a more random fashion

High-reward trapliner (traveling exploitation)

Hummingbird that visits dispersed, nectar-rich flowers in repeated circuits

Low-reward trapliner (traveling exploitation)

Hummingbird that visits dispersed, low-reward flowers in repeated circuits

Floral specialist

Hummingbird that has coevolved to rely on specific flowers via bill-corolla matching

Territorialist (stationary interference)

Hummingbird that defends patches of flowers

Territory parasite

Hummingbird that parasitizes a territorialist's resources

Large marauder

Large hummingbird that ignores the attacks of a smaller territorialist

Small filcher

Small hummingbird that feeds surreptitiously in areas generally unattended by a territorialist

Maneuverability

Ability to change speed and direction

Wing disc loading (WDL)

Ratio of body weight (N) to the circular area swept out by the wings

Wing loading

Ratio of body weight to wing area

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