

Under pressure: the behavioral richness of hummingbirds in competitive landscapes

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Abstract

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Competition for resources is a unifying struggle across the animal kingdom. Hummingbirds, facing fierce races for nectar while balancing record-high metabolic demands, are an exceptional case study for this conundrum, and the decisions that these tiny birds must make to survive each day are complex. Where to travel, and which rival is worth attacking? Does it pay off to stay near home, saving energy for inevitable battle, or to fly further afield—facing new perils—to find food? With new approaches and miniature biologgers, we can get a glimpse into how each individual hummingbird might approach these challenges, even and especially when surrounded on all sides by competitors. I have three chapters in my dissertation dedicated to this concept: **(1)** A published review of the principal strategies with which hummingbirds commute within landscapes (“traplining”) or monopolize flowers (“territoriality”) when competing for finite resources, and the flexibility with which they adapt their behavior while doing so. This review also offers predictions regarding the traits we expect to be associated with these main strategies, along with proposed methods of testing them. **(2)** An ethical study of how hummingbirds behave when equipped with backpack-style biologgers, in order to ensure that the radio-trackers—which we would use to study hummingbird movement and foraging strategies in the wild—do not drastically alter the very behaviors we would hope to measure in the first place. This chapter was based on a time-budget

experiment in which each bird underwent both a tagged and an untagged treatment; we found that birds spent significantly more time preening when tagged. **(3)** A case study showcasing how differently six tagged hummingbird species can utilize an array of feeders while coexisting under increasingly competitive conditions at an agricultural-forested site in Colombia. In this experiment, we progressively removed and reinstated feeders equipped with radio-frequency identification (RFID) antennas and found that, as scarcity mounted and the birds were funneled onto fewer and fewer options, individuals and species that had little time at the feeders to begin with were more likely to cease visiting them entirely. Overall, my dissertation offers an integrative perspective with which to examine hummingbird foraging and its mutability to the surrounding energetic, risk, and competitive landscapes, accounting for not only morphology and biomechanics, but also the effects of the tools that we use to investigate these strategies, as well as the unique behavioral signature of each individual hummingbird in question.

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Dissertation overview

Hummingbirds (Trochilidae) comprise a riveting avian family that has long captured the imagination and attention of humankind. The smallest birds in the world, these tiny pollinators are legendary for their array of iridescent colors and remarkable abilities. Indeed, hummingbirds featured so heavily in Mayan creation stories that scholars coined the term “hummingbird myths” to subsume a host of archetypal tales in which a hero would magically transform one of these birds, in order to bring about divine marriage between himself and the daughter of an earth god (Mazariegos 2010). The Mexican god Huitzilopochtli (which translates to “hummingbird on the left”), meanwhile, was also described as wearing a hummingbird disguise; hummingbirds’ capacity for “deadening” and “awakening” through torpor; their capacity for long-distance migration like that of the Aztecs; their mutualistic relationship with flowers (which were associated with warriors), and their swiftness in flight and subsequent success in combat were all mythologically tied to this deity (Montero Sobrevilla 2020). Of course, humanity’s captivation with these birds has not always been positive: in the Victorian period, millions of hummingbirds were taxidermized for both personal collections and as glittering fashion accessories (Murfin 2026); even now, illegal trade of hummingbirds persists in Mexico, with their bodies being used for *chuparosa* “love charms” (Trail 2022). At large, hummingbirds spark positive public perceptions today for their distinctive traits (Andrade et al. 2022).

Amongst scientists, too, hummingbirds have exerted a powerful fascination, for many of the same reasons. Their versatility—evidenced by their spanning Canada to Patagonia, sea level to the high Andes, metropolises to cloud forests (English et al. 2021)—and sheer morphological variety across their ~366 representative extant species (Leimberger et al. 2022) present a compelling case study for adaptation and selective pressures (e.g., Rappole and Schuchmann 2003; Stiles 2008; Abrahamczyk and Kessler 2015). Relative to their body mass and length, hummingbirds have the highest metabolic rates (Suarez 1992) and movement velocities (Clark 2009) recorded amongst vertebrates; relative to the telencephalon, they have the largest hippocampal formations (critical for spatiotemporal memory) documented within birds (Ward et al. 2012). What is more, they are the only birds capable of sustained wing-derived hovering, thanks to their unique ability to invert their wings during the upstroke (Hedrick et al. 2011) and their remarkably high proportions of supracoracoideus muscles (Deeming 2023). In short, the Trochilidae family is exceptional in many respects, and has garnered a great deal of research already.

On the behavioral front, however, there is still much to explore. How hummingbirds navigate competition has been of particular interest to ecologists over the years: not only do these pollinators rely on nectar to fulfill their energetic demands—a resource that, in natural systems, is ephemerally available in minute volumes and spatially scattered as per the plants that produce it—but they can also congregate in huge numbers at resource hotspots, leading to intense races and battles for floral access (Sargent et al. 2021). By employing different strategies, hummingbirds can find ways to overcome competitive pressures (or at least mitigate or avoid them). But what constitutes a “strategy”? The hummingbird foraging literature is rooted in a handful of archetypal behavioral syndromes first defined in relation to hummingbirds over 50 years ago (e.g., Pitelka 1942; Janzen 1971; Stiles 1975), when researchers lacked the technology to track the movement and resource visitation of unique individuals and largely based their characterizations on observations of only a few birds per study, as opposed to direct evidence or quantitative data (see Tello-Ramos et al. 2015). These concepts have been developed relatively little since and remain the default framing

for many researchers to this day (e.g., Rombaut et al. 2022; Ríos-Orjuela et al. 2026), with hummingbirds still classified according to these strategies at the species, sex, or even clade level (Tello-Ramos et al. 2015; Sargent et al. 2021; Falk et al. 2025 preprint). Yet hummingbirds display remarkably flexible behavior depending on the energetic and risk landscapes around them, abandoning or modifying their tactics as needed (Kodric-Brown and Brown 1978; Hixon et al. 1983; Stiles 1985; Carpenter 1987; Justino et al. 2012; Sargent et al. 2021). The emerging perspective is thus that hummingbirds may instead operate on a spectrum of foraging strategies (Sargent et al. 2021), or even that they have a “menu” of foraging options from which to select, depending on the context in which they find themselves (Altshuler et al. 2004).

My research largely focuses on exploring this potential spectrum. With the advent of ultra-miniaturized biologging devices, we can now record high-resolution spatiotemporal data for individual hummingbirds of *any* species—which, up until several years ago, was reserved to only the larger species of hummingbirds (Hadley and Betts 2009; Williamson and Witt 2021; Sargent et al. 2026)—and thereby tease apart the characteristics of these different strategies, along with the traits, mechanisms, and conditions that shape them (Sargent et al. 2021). Of course, we must also ensure that the biologgers do not distort the behaviors that we hope to measure in the first place (e.g., Sargent et al. 2026). My dissertation thus operates along multiple axes (conceptual, ethical, and experimental) to deepen our understanding of the hummingbird foraging continuum, and how hummingbirds respond to competition on all sides, in a safe and empirical manner. My three chapters are as follows:

Chapter I: Locomotion and energetics of divergent foraging strategies in hummingbirds: a review. This chapter is my integrative, published review of the different ways that hummingbirds purportedly monopolize or seek to deplete flowers before their competitors when competing for finite resources. The current hummingbird foraging literature is almost entirely structured around two specific strategies: territoriality (in which a hummingbird will engage in interference competition to defend smaller, concentrated patches of more generalized resources through high-powered aerial combat) and traplining (in which a hummingbird will engage in exploitation competition to commute in efficient circuits to dispersed, more specialized resources, without defending them). I revisit the historical studies that shaped this ostensible dichotomy, as well as the current studies that have relied upon it, and argue that hummingbird behavior is in fact highly flexible and shaped by the competitive landscape, and therefore more likely to exist on a continuum. Through a biomechanical and morphofunctional lens, I examine the locomotor and energetic traits that dictate hummingbird foraging, and provide predictions for how body size, burst power, maneuverability, flight muscle mass, and basal metabolic rate might relate to both territoriality and traplining. Drawing on tried-and-true methods (e.g., wing loading, respirometry) alongside recent technological advances (e.g., biologging, 3D flight tracking), I propose methods to test each prediction, to enhance our understanding of the selective pressures shaping these potential extremes of a hummingbird foraging spectrum.

Chapter II: Variable evidence of radio-tag backpacks affecting hummingbird time budgets in captivity. Despite the rapid miniaturization of biologgers—enabling wildlife-tracking research on increasingly smaller taxa—and their corresponding ubiquity in the field of ecology, the ethical study of these devices has not kept pace. In this chapter, I assess whether backpack-style radio-transmitters significantly affect the behavior of hummingbirds in captivity. I designed a 3-hour time-budget experiment within a flight arena in Colombia to compare how much time 25 Black-

throated Mangoes (*Anthracothorax nigricollis*) each spent flying, hover-feeding, preening, and perching when tagged versus untagged; furthermore, I complemented this experiment with an aviary-style “entanglement” test, to determine whether the birds would snag on vegetation while harnessed with the radio-transmitter. Hummingbirds spent significantly more time preening when tagged; they also flew significantly more in their second treatment (tagged and untagged treatments were randomized), fed significantly longer if they were lighter, and preened significantly more in the afternoon than the morning. Birds did not get entangled within the aviary, even during overnight trials. My experimental model, which relied on an inexpensive and portable setup that is suitable for remote field conditions, is relatively straightforward to fine-tune to other small avian taxa and device types and can be applied more broadly as a pre-deployment “behavioral validation” checkpoint—a sorely needed addition to the field of biologging ethics.

Chapter III: The unequal cost of scarcity: how individual hummingbirds across an assemblage respond to experimental feeder removal. This final chapter is the empirical culmination of my dissertation and many years of preparatory work: a 21-day, individual-level experiment within a thriving hummingbird assemblage in the Colombian Andes. Using a network of 16 RFID-enabled feeders and a mirrored “removal and reinstatement” design (7 three-day periods: 16 → 12 → 8 → 4 → 8 → 12 → 16 feeders), I examined the impacts of variable artificial resource availability and a subsequent competitive bottleneck on the feeder-visitation patterns of 109 individuals spanning six species. Through eight *a priori* questions operating along individual, species, and assemblage levels, I found that baseline access—a bird’s share of feeder time in the first three-day period, prior to any experimental manipulation—remained a stable trait as the study progressed. Indeed, this metric predicted several other “downstream” results, with low-access birds more likely to drop out during the bottleneck (and not necessarily return), be more absent from feeders during energetically critical morning and evening windows, visit feeders less often and in shorter bouts, and exhibit less repeatable behavioral patterns. Thus, the costs of scarcity and corresponding competition did not fall equally on all birds: low-access individuals and certain species bore the brunt of the experiment, suggesting that hummingbird assemblages might buffer against rapid losses of resources through hierarchical filtering.

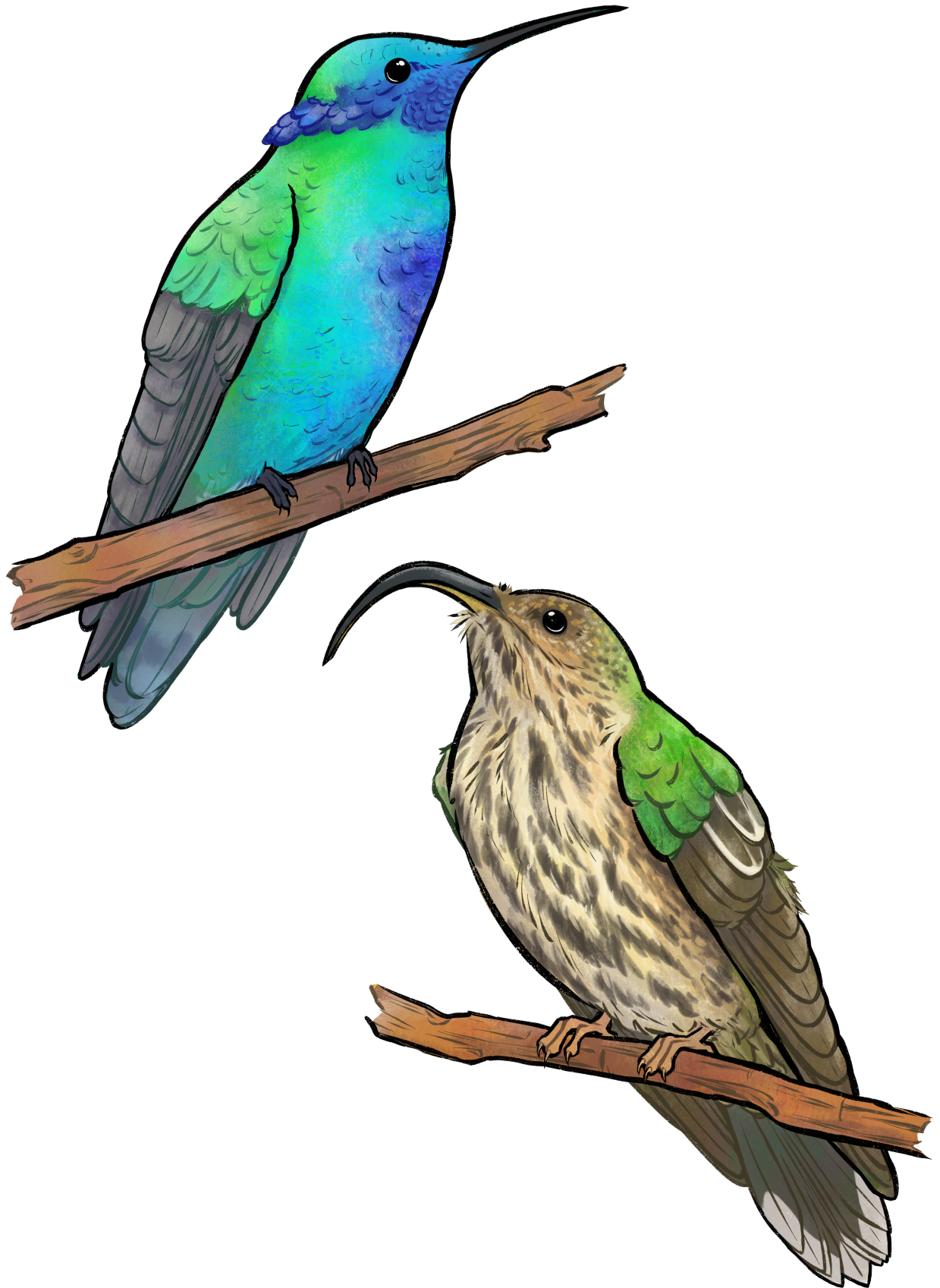
As a whole, my dissertation offers an integrative lens through which to reexamine the foraging of these critical vertebrate pollinators. The strategies employed by hummingbirds are shaped not only by morphology, metabolism, and biomechanics, but also by individual variation and the surrounding energetic and risk landscapes; if we are to properly tease apart the behavioral spectrum, we therefore must implement a wide variety of tools and approaches in the coming years. I have focused on developing custom roadmaps and experiments that utilize cutting-edge technology to begin this process. My work has direct implications for the ethical practices with which we study small, flighted animals, as well as the management of artificial resources: with maintaining bird feeders a global pastime, and natural resources dwindling worldwide, now more than ever we must determine how individuals, species, assemblages, and even full communities will respond to unexpected scarcity—and the shape that the ensuing competition will take.

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(2):333–347. <https://doi.org/10.1007/s10336-014-1146-5>

- Altshuler DL, Stiles FG, Dudley R. 2004. Of Hummingbirds and Helicopters: Hovering Costs, Competitive Ability, and Foraging Strategies. *The American Naturalist*. 163(1):16–25. <https://doi.org/10.1086/380511>
- Andrade R et al. 2022. Species traits explain public perceptions of human–bird interactions. *Ecological Applications*. 32(8):e2676. <https://doi.org/10.1002/eap.2676>
- Carpenter FL. 1987. Food Abundance and Territoriality: To Defend or Not to Defend? *Am Zool*. 27(2):387–399. <https://doi.org/10.1093/icb/27.2.387>
- Clark CJ. 2009. Courtship dives of Anna’s hummingbird offer insights into flight performance limits. *Proceedings of the Royal Society B: Biological Sciences*. 276(1670):3047–3052. <https://doi.org/10.1098/rspb.2009.0508>
- Deeming DC. 2023. Allometry of the pectoral flight muscles in birds: Flight style is related to variability in the mass of the supracoracoideus muscle. *Journal of Zoology*. 319(4):264–273. <https://doi.org/10.1111/jzo.13043>
- English SG, Bishop CA, Wilson S, Smith AC. 2021. Current contrasting population trends among North American hummingbirds. *Sci Rep*. 11(1):18369. <https://doi.org/10.1038/s41598-021-97889-x>
- Falk JJ, Sargent AJ, Medina J, Rico-Guevara A. 2025. The daily life of a hummingbird: High-throughput tracking shows a spectrum of feeding and movement strategies. 2025.02.25.640146 [accessed 2026 May 14]. <https://www.biorxiv.org/content/10.1101/2025.02.25.640146v1>. <https://doi.org/10.1101/2025.02.25.640146>
- Hadley AS, Betts MG. 2009. Tropical deforestation alters hummingbird movement patterns. *Biol Lett*. 5(2):207–210. <https://doi.org/10.1098/rsbl.2008.0691>
- Hedrick TL et al. 2011. Morphological and kinematic basis of the hummingbird flight stroke: scaling of flight muscle transmission ratio. *Proc Biol Sci*. 279(1735):1986–1992. <https://doi.org/10.1098/rspb.2011.2238>
- 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(3):366–391
- Janzen DH. 1971. Euglossine Bees as Long-Distance Pollinators of Tropical Plants. *Science*. 171(3967):203–205
- Justino DG, Maruyama PK, Oliveira PE. 2012. Floral resource availability and hummingbird territorial behaviour on a Neotropical savanna shrub. *J Ornithol*. 153(1):189–197. <https://doi.org/10.1007/s10336-011-0726-x>
- Kodric-Brown A, Brown JH. 1978. Influence of Economics, Interspecific Competition, and Sexual Dimorphism on Territoriality of Migrant Rufous Hummingbirds. *Ecology*. 59(2):285–296. <https://doi.org/https://doi.org/10.2307/1936374>
- Leimberger KG et al. 2022. The evolution, ecology, and conservation of hummingbirds and their interactions with flowering plants. *Biological Reviews*. 97(3):923–959. <https://doi.org/10.1111/brv.12828>
- Mazariegos OC. 2010. Of Birds and Insects: The Hummingbird Myth in Ancient Mesoamerica. *Ancient Mesoamerica*. 21(1):45–61. <https://doi.org/10.1017/S0956536110000155>
- Montero Sobrevilla I. 2020. The Disguise of the Hummingbird: On the Natural History of Huitzilopochtli in the Florentine Codex. *Ethnohistory*. 67(3):429–453. <https://doi.org/10.1215/00141801-8266434>

- Murfin A. 2026. Bird[s] Matter: The Case of Hummingbirds. In: Murfin A, Lantz VP, Bucheli S, editors. *Animal Fashions: Colonialism, Collecting, and Gender*. Springer Nature Switzerland; p 35–58 [accessed 2026 June 20]. https://doi.org/10.1007/978-3-032-06191-1_2
- Pitelka FA. 1942. Territoriality and Related Problems in North American Hummingbirds. *The Condor*. 44(5):189–204. <https://doi.org/10.2307/1364129>
- Rappole JH, Schuchmann K-L. 2003. Ecology and Evolution of Hummingbird Population Movements and Migration. In: Berthold P, Gwinner E, Sonnenschein E, editors. *Avian Migration*. Springer; p 39–51. https://doi.org/10.1007/978-3-662-05957-9_3
- Ríos-Orjuela JC et al. 2026. Scaling and foraging behaviour drive the evolution of humeral shape in hummingbirds. *Proc Biol Sci*. 293(2069):20260275. <https://doi.org/10.1098/rspb.2026.0275>
- Rombaut LMK et al. 2022. The evolution of the traplining pollinator role in hummingbirds: specialization is not an evolutionary dead end. *Proc Biol Sci*. 289(1967):20212484. <https://doi.org/10.1098/rspb.2021.2484>
- Sargent AJ et al. 2026. Variable evidence of radio-tag backpacks affecting hummingbird time budgets in captivity. *Anim Biotelemetry*. 14(1):11. <https://doi.org/10.1186/s40317-026-00446-4>
- Sargent AJ, Groom DJE, Rico-Guevara A. 2021. Locomotion and Energetics of Divergent Foraging Strategies in Hummingbirds: A Review. *Integrative and Comparative Biology*. 61(2):736–748. <https://doi.org/10.1093/icb/icab124>
- Stiles F. 2008. Ecomorphology and phylogeny of hummingbirds: Divergence and convergence in adaptations to high elevations. *Ornitologia Neotropical*. 19:511–519
- Stiles FG. 1975. Ecology, Flowering Phenology, and Hummingbird Pollination of Some Costa Rican Heliconia Species. *Ecology*. 56(2):285–301. <https://doi.org/https://doi.org/10.2307/1934961>
- Stiles FG. 1985. Seasonal Patterns and Coevolution in the Hummingbird-Flower Community of a Costa Rican Subtropical Forest. *Ornithological Monographs*. (36):757–787. <https://doi.org/10.2307/40168315>
- Suarez RK. 1992. Hummingbird flight: Sustaining the highest mass-specific metabolic rates among vertebrates. *Experientia*. 48(6):565–570. <https://doi.org/10.1007/BF01920240>
- Tello-Ramos MC, Hurly TA, Healy SD. 2015. Traplining in hummingbirds: flying short-distance sequences among several locations. *Behav Ecol*. 26(3):812–819. <https://doi.org/10.1093/beheco/arv014>
- Trail PW. 2022. Dying for love: Illegal international trade in hummingbird love charms. *Conservation Science and Practice*. 4(6):e12679. <https://doi.org/10.1111/csp2.12679>
- Ward BJ et al. 2012. Hummingbirds have a greatly enlarged hippocampal formation. *Biol Lett*. 8(4):657–659. <https://doi.org/10.1098/rsbl.2011.1180>
- Williamson JL, Witt CC. 2021. A lightweight backpack harness for tracking hummingbirds. *Journal of Avian Biology*. 52(9) [accessed 2022 Oct 31]. <https://onlinelibrary.wiley.com/doi/abs/10.1111/jav.02802>. <https://doi.org/10.1111/jav.02802>



Illustrations by AsterWild Art

Chapter I: 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.

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 exploitation**, 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 trapliners (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 traplining 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.

Declarations

Data availability statement.

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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 (*Helioaster 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 Value1. *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, Mickley 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 theresiae*). *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.

Glossary and figures

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

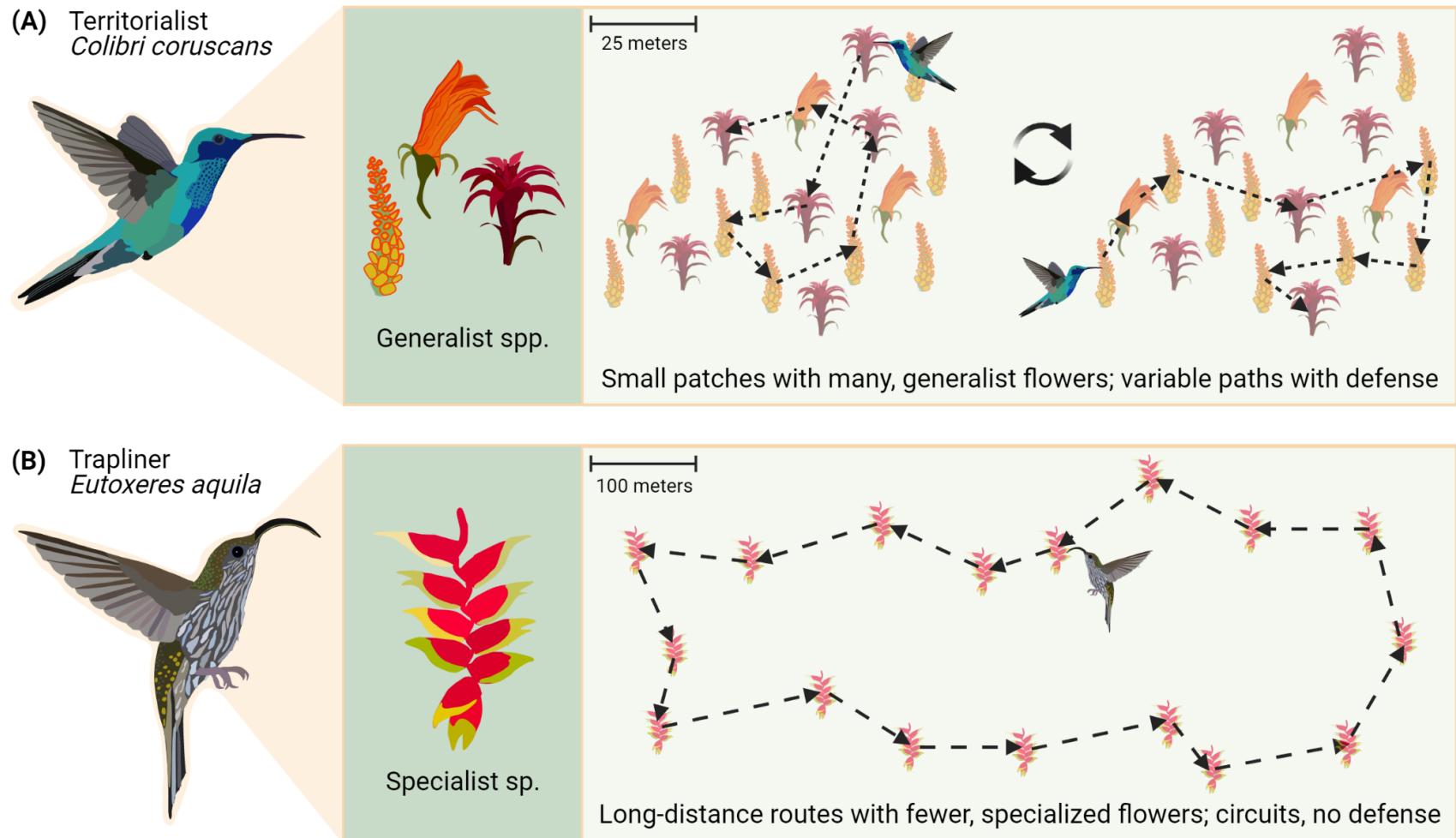
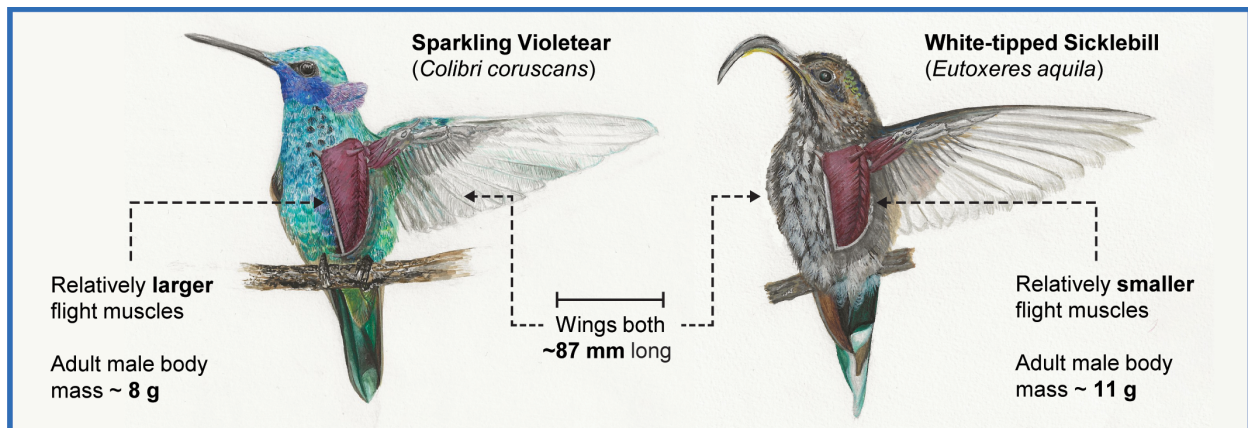


Figure 1. Traditional understanding of major hummingbird foraging strategies. (A) Quintessential territorialist represented by the Sparkling Violetear (*Colibri coruscans*), which feeds from numerous generalist plants, including *Elleanthus* (left), *Siphocampylus* (middle), and *Guzmania* (right). (B) 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.

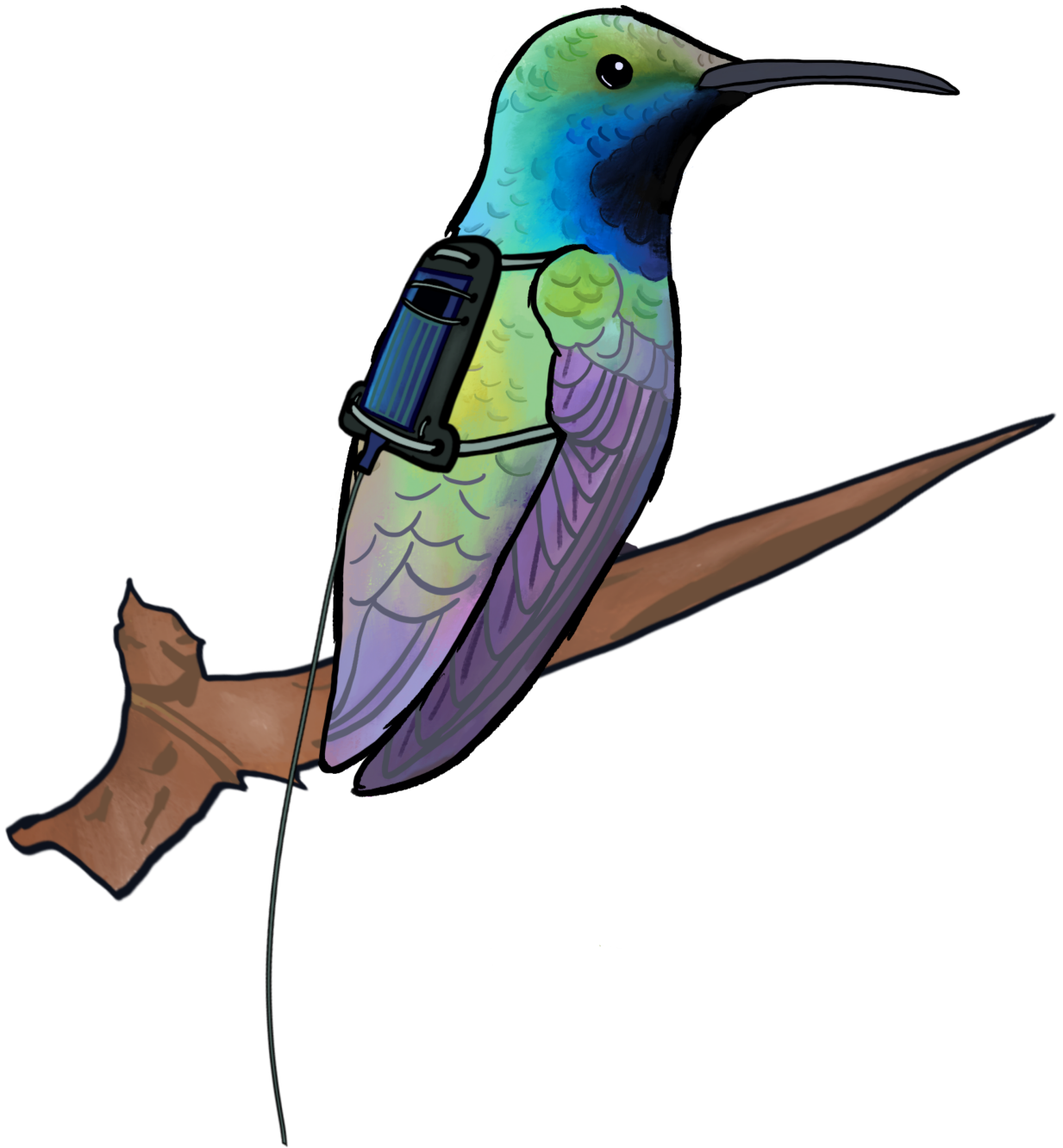


Illustration by Alyssa J. Sargent

Chapter II: Variable evidence of radio-tag backpacks affecting hummingbird time budgets in captivity

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Abstract

Background: With wildlife-tracking devices miniaturizing rapidly to enable ever-more research on ever-smaller taxa, there is a newfound urgency for affordable, field-accessible biologging ethics studies. We designed a 3-hour time-budget experiment to investigate how radio-transmitter backpacks affect hummingbirds' behavior in Colombia.

Methods: Using a large flight arena, we individually filmed 25 Black-throated Mangoes (*Anthracothorax nigricollis*) under two randomized treatments, tagged and untagged, to characterize and quantitatively compare behavior. We created time-budget breakdowns of our behaviors of interest—flying, hover-feeding, preening, and perching—then fit a series of linear mixed-effects models to determine the effects of tagging and additional experimental and environmental variables on behavior. We also designed an aviary-style “Entanglement Experiment” (n = 30) to determine if any individuals would snag on vegetation while equipped with the backpack harness, and tested 6 additional birds in this enclosure overnight for any longer-term negative effects.

Results: When tagged, individuals on average spent overall less time flying (with fewer and shorter bouts); and more total time feeding, preening (with more and longer bouts in both cases), and perching (with fewer but longer bouts)—however, this difference in total duration was only statistically significant in the case of preening. Our best-supported models also highlighted the importance of the following additional effects: whether or not the bird was undergoing its first or second 1.5-hour treatment (birds flew significantly more in their second treatment), bird mass (lighter birds fed significantly longer overall), and the time of day (birds preened significantly more in the afternoon than the morning, and more in the evening than the afternoon). No individuals in this captive study became entangled in vegetation or exhibited any adverse overnight effects from harness wear.

Conclusions: In our captive study, radio-transmitter backpacks significantly affected the amount of time that hummingbirds spent preening, and additional environmental variables helped explain behavioral differences in each bird's treatments. While being in a confined space doubtlessly affected the behavior of individuals, our experimental model is relatively straightforward to fine-tune to other small avian taxa and is suitable for remote conditions, providing a useful basis for examining species-specific effects of biologging prior to starting field studies.

Background

As biologging devices become ever-smaller and increasingly prevalent, the number of studies on animal movement, behavior, and physiology has risen substantially, providing a wealth of environmental and ecological information [1,2]. This surge has brought **biologging ethics**—the study of animals' welfare while equipped with auxiliary devices—to the forefront of automated tracking concerns [3–7], and for good reason. Biologgers have been tied to a slew of negative effects, impacting behavior [8], sensory organs [9], foraging [10], reproduction [10–12], energetics [10,13,14], and survival [12,15,16].

Device mass is commonly considered the root of many of these issues and, as a means of addressing them, many biologging studies conform to the “3–5% rule”: a widely accepted ethical standard wherein devices must weigh below 3–5% of the animal's body mass [17–19]. Many researchers have, however, criticized this rule for its lack of evidential support [6,11,16,20,21] and its overly simplistic approach [21]. *How* and *where* a biologger is attached to an animal can also present complications [15,16,22]—and the 3–5% rule accounts for neither biomechanics (e.g., relative wing area to body size) nor life history (e.g., aquatic vs. terrestrial lifestyles [3,16]). Volant animals, in particular, must compensate for the additional mass and drag of tracking devices by adjusting their flight kinematics (e.g., increasing stroke amplitude and/or wingbeat frequency [23,24]), which not only increases energy expenditure, but also reduces flight performance [6,11,25,26].

Nevertheless, many avian biologging studies do not report or test for tag effects [4]; there is still a pressing need for species-specific experimental designs [27,28]. Though tools such as respirometers and wind tunnels can provide highly detailed information on device effects as they relate to physiology, they do not provide any information regarding birds' potential for entanglement in vegetation or longer-term impacts (e.g., multi-hour assessments across which many more behaviors can be evaluated); furthermore, this equipment can be both costly and complex [29,30], and is not always suitable for the remote field settings where many automated tracking studies take place [2]. Conversely, **time budgets** (which break down the proportion of time an animal spends conducting various behaviors) can act as a useful, field-accessible tool for biologging welfare studies. As a biologger may increase the energy needed to perform a specific activity, or prevent it entirely [3], time budgets allow researchers to compare between tagged and untagged individuals from the same population [4,5,28].

Hummingbirds are notoriously energy-constrained birds [31–33]; as such, researchers applying auxiliary devices to hummingbirds should consider welfare and time budgeting of critical importance (see [28] for a fundamental example). It is well-established that hummingbirds are capable of remarkable feats of strength: lifting well over their body mass in maximum performance tests (e.g., [34,35]); sustaining flight in heavy rain, a mere 20 seconds of which can increase their body mass by 20% [36]; and, in the case of females, developing and carrying eggs up to 15% of their own body mass [37]. However, these displays of burst or short-term power may not be indicative of more prolonged weight-carrying capabilities, and/or the ability to fly with external aerodynamic impediments [2]. Biologgers have only recently miniaturized enough to tag these tiny

birds [28,38–41], and ethical studies of their effects have been sparse [28]. The fresh introduction of backpack harnesses to hummingbird research [39] has allowed for an advantageous combination: tags with lengthy detection distances (unlike passive integrated transponders [42,43]) that can be deployed for far longer periods than those affixed with glue (such as battery-powered radio-transmitters [38]). Yet hummingbird backpacks are still relatively novel, and we lack any ethical quantifications of how they affect the behavior of individual birds.

With the hypothesis that wearing tags is costly for hummingbirds [28], we designed a time-budget experiment to determine the behavioral impacts of a backpack harness with a custom chassis, along with a field-accessible test to examine hummingbirds' propensity to get entangled in vegetation while fitted with it (see [44] for a documented case of entanglement and mortality in Hawaiian honeycreepers when equipped with radio-transmitters). In this study, we compared the behavior of hummingbirds when they were equipped with a radio-transmitter versus when they were not. We predicted that, when tagged, individuals would: **(1)** fly less to reduce energetic expenditure [28]; **(2)** perch more for the same reason; **(3)** feed more to increase energetic intake from *ad libitum* syringes (but see [45] for the opposite results in a free-living study of goldeneyes); and **(4)** preen more in attempts to physically remove the radio-transmitters, despite the energetic cost [11,45–47].

Methods

Study overview.

After performing a pilot-iteration of this study in Ecuador (detailed in **Supplementary Material: Ecuador Pilot, Harness and Device Chassis Design**, and **Table S1**), we conducted all of our experiments in the dry season of August and September 2022 at Centro de Investigación Colibrí Gorriazul (hereafter referred to as “Gorriazul”) in Colombia. Gorriazul is situated at roughly 1,700 m elevation, midway up the western slope of the Eastern Cordillera of the Colombian Andes, in a matrix of pristine rainforest and agricultural properties (4.38168°, -74.35136°).

We chose to work with the Black-throated Mango (*Anthracothorax nigricollis*), on account of its large body size (8.10 ± 0.53 g) and significant abundance onsite; to further reduce confounding effects that may impact behavior, we worked selectively with adult birds that had typically male-associated plumage. It is worth noting that there are recorded cases of female polymorphism —“male-like females”—within this species [48–50], but we lacked the resources to genetically sex individuals. We captured all birds using baited drop-net traps [51], either processing them immediately post-capture or rapidly placing them in bird bags as a form of sensory deprivation to reduce stress [3].

Tagging procedure.

We first identified, aged (based on plumage and bill corrugations), sexed (based on plumage), took baseline morphometric measurements for, and scored the body conditions of each newly captured bird [51]. Next, we injected each individual with an interscapular, subcutaneous passive integrated transponder (BioMark)—also referred to as a radio-frequency identification (RFID) tag—and closed the insertion site with surgical glue (VetBond) as described by Bandivadekar et al. [42]. These 8 mm, 35 mg RFID tags proved to be more informative identifiers than tarsal bands—for

which hummingbird-specific tools are prohibitively difficult to access or fabricate, especially given the lack of methods standardization for tropical species. After implantation, we released each bird and monitored its return to our feeders, which were equipped with short-range RFID antennas. By cross-checking RFID readings with capture data, we selectively recaptured individuals after a minimum of 7 days, weighed them, and verified that insertion wounds had healed. Only then did we proceed with further experimentation, as described in the following sections.

To equip an individual with a radio-transmitter (Cellular Tracking Technologies “LifeTag”) backpack harness (**Fig. 1**), we replicated the process of Williamson and Witt [39] and spent approximately 5–7 minutes per harness application (restraining the birds using a strip of cloth and a small clip for the final double surgeon’s knot, **Supplementary Material: Fig. S1**). See **Table 1** for all body mass and tag specifications. When prepared with our custom chassis and attachment materials, total attachment mass averaged 0.44 ± 0.02 g. See **Supplementary Material: Harness and Device Chassis Design** for an in-depth description of our chassis fabrication process, which we optimized for ultra-lightweight and durable field applications, as well as a discussion of its practical benefits. We focused our experiment solely on the biologging ethics of these radio-transmitters, given that RFID tagging is a relatively common hummingbird marking technique and has therefore been more thoroughly explored [35,42,43,52–55].

Experimental overview.

Testing each hummingbird individually and directly post-capture (i.e., no holding time between capture and experimentation), we conducted two different types of radio-transmitter backpack experiments on Black-throated Mangoes. The first consisted of a 3-hour, time-budget “Behavior Experiment” ($n = 27$) in a flight tent pitched indoors to monitor hummingbird mass, feeding, and behavior in a controlled space. The second consisted of 1-hour ($n = 30$) or overnight ($n = 6$) “Entanglement Experiment” in an aviary-style tent pitched outdoors to monitor hummingbirds’ flight and behavior when simultaneously exposed to natural vegetation. After completing a Behavior Experiment, if there was adequate time to finish all work at least 1 hour prior to local sunset—to provide each individual sufficient time to feed and readjust in the wild before roosting—we immediately proceeded to test the bird in the 1-hour Entanglement Experiment (birds tested overnight did not undergo additional experimentation beforehand). As such, we retained birds in captivity for either 1 hour (Entanglement Experiment only, $n = 8$); 3 hours (Behavior Experiment only, $n = 5$); 4 hours (Behavior and Entanglement Experiments, $n = 22$); or, in the case of birds tested overnight ($n = 6$), up to 24 hours. Below, we break down each experimental approach in detail.

Behavior experiment design.

Our flight arena was a six-person Coleman tent (3.0 x 2.4 x 1.8 m) that we pitched directly inside the research center. Inside, we placed a tripod mounted with two Raspberry Pi load cells, one for a feeder syringe (provided sucrose solution was 15–20% w/w, measured with a refractometer at the beginning of each trial) and one for the only perch available (**Supplementary Material: Fig. S2**). We also equipped the tent with **a**) a GoPro Hero 7 Black (720p resolution) in the side pocket to surveil each bird via live feed, to ensure that it fed and perched successfully without displaying signs of distress (see below); and **b**) a thermometer with a wire sensor threaded through the door, to monitor interior temperature and ensure that it did not get too hot throughout the day. On average, our flight arena was only 2.07 ± 0.83 °C warmer than ambient temperature during our tests (as

determined via our Ambient Weather Station on-site), and remained at least 5 degrees below the 32 °C maximum recommended by Russell et al. [51]. We separated the tent from researchers via a dividing sheet (draped from the ceiling) in the middle of the room, to prevent visual stimulation and further stress for the birds [3]. We used a Minolta MN80NV camcorder (1080p resolution, 30 fps) and a backup JVC camera (1080p resolution, 60 fps), which performed well without overheating during our extended filming periods in tropical conditions. Additionally, owing to substantial drift from the load cells, we elected to weigh each individual and the syringe before and after each experiment; we also checked all individuals for any sign of harness-induced skin abrasion at the conclusion of all testing.

To establish baseline behavior in captivity and quantify the “degree of departure from the norm” [3] when tagged, we tested each individual ($n = 27$) inside the flight arena under two treatments, randomized in order: tagged and untagged with a radio-transmitter harness (following similar methodologies established by Zenzal et al. [28]). After offering each individual nectar from a handheld syringe to prompt its flower-like recognition, we began the experimental procedure: for each 1.5-hour treatment, we released the bird into the arena, allowed it 30 minutes to acclimate, and then filmed its behavior for 1 hour. We defined *acclimation failure* as a bird displaying signs of distress (remaining stationary on tent floor or gaping bill, as characterized by Russell et al. [51]), and/or an inability to identify either the nectar-filled syringe or the perch we provided, in these first 30 minutes. In such cases, we terminated the trial early, then hand-fed and released the individual.

Behavior experiment analysis.

Scoring behaviors.

We analyzed all treatment videos frame-by-frame using the Behavioral Observation Research Interactive Software (BORIS) [56], which creates time-budget breakdowns from logged behaviors of interest. Over the course of each given treatment’s (tagged or untagged) observation period, we quantified a bird’s flight, hover-feeding, preening, and perching through the metrics of total duration, bout number (number of times a behavior was performed), and bout duration (length of each individual bout). Frame-counting could begin while the bird was conducting any behavior (e.g., mid-flight). We defined the start and end of each ethological category as the first and last frames, respectively, in which the bird visibly changed its behavior. As such, we considered the bird to be “hover-feeding” whenever its bill was in contact with the syringe feeder, “preening” at any time that its bill was in contact with its feathers (following Zenzal et al. [28]), “perching” at any point when its feet were in contact with the perch (both during and between preening bouts), and “flying” whenever the bird was airborne but not hover-feeding (including any flights to the syringe, or between feeding bouts); see **Supplementary Material: Video S1** for examples. We conducted all remaining analyses using R version 4.3.1 [57].

To determine the reliability of our ethological video analyses and the protocols with which we differentiated behavior types, we used the *irr* package to conduct an inter-rater reliability analysis [58], which is used to quantify the level of consistency between different raters (observers). As per Harvey [59], continuous data call for an intra-class correlation coefficient; we calculated this statistic using a consistency type, single-measure, two-way random-effects model for 24 measurements (6 raters scoring the same 4 videos), each of which we checked for normality. Here, we compared raters’ calculated durations (of flying, hover-feeding, preening, and perching) for the subset of videos in a single statistical test [59].

Tag effects and model selection.

Our predictions were as follows: when tagged, individuals would overall: **(1)** fly less, **(2)** perch more, **(3)** hover-feed more, and **(4)** preen more. Using the *lme4* [60], *lmerTest* [61], and *glmmTMB* [62] packages, we fit a series of general and generalized linear mixed-effects models to characterize the relationship between how much time (total duration) birds spent performing a given behavior and radio-transmitter backpacks, as well as additional environmental or experimental variables. These included: **treatment type** (2 levels: tagged and untagged); individual's **mass** at the start of the trial (continuous, in grams); **treatment number** (2 levels: treatment 1 and treatment 2); tent's average internal **temperature** for the treatment (continuous, in Celsius); **percent sucrose** of the provided nectar throughout the trial (continuous); and **period of day** wherein the majority of the treatment took place (3 levels: morning, 6:00–11:59; afternoon, 12:00–15:59; and early evening, 16:00–on). Compared to a null model that only incorporated a random effect of individual (which we included in all other models), our global model was as follows:

$$\text{behavior} \sim \text{treatment type} * \text{treatment number} + \text{weight} + \text{temperature} + \\ \text{period of day} + \text{sucrose concentration} + (1|\text{individual})$$

Where *behavior* was flying, hover-feeding, or preening (we did not model time spent perching, which was the inverse of the combined durations of flying and hover-feeding; the behaviors are mutually exclusive). Given that Zenzal et al. [28] found a significant interaction between their experimental order and whether a bird was tagged, we incorporated an interaction between treatment type and number in our own models (and also tested the two parameters additively). We ran this global model structure for each behavior, then tested simpler models stepwise to reduce the model to its simplest form.

Using the *DHARMA* package [63], we checked for the most appropriate model error structure for each behavioral category through dispersion, outlier, homoscedasticity, and zero-inflation tests; we also assessed the structure and distribution of our residuals with QQ-normality and residual vs. fitted-value plots. While a Gaussian distribution provided the optimal fit for flight models, feeding and preening models were best suited for a tweedie distribution. Furthermore, feeding models were zero inflated (in 8% of the observation periods, individuals did not feed at all), and through likelihood ratio testing we confirmed that model fit was significantly improved with a zero-inflation parameter. This was not the case for preening, despite more zero values (44%); here, a zero-inflation parameter worsened model fit.

We conducted all model selection using Akaike's information criterion corrected for small sample sizes (AICc), considering any model within 2 ΔAICc of the top-supported model competitive. For top models, we present the p-values (for which we used a Benjamini-Hochberg multiple-testing correction [64]) and effect sizes (β -estimates) of individual parameters; if their 95% confidence intervals did not overlap zero, we considered them to be significant influences on behavior [65].

Entanglement experiment design.

Our aviary consisted of a large, open-floored, mesh-walled tent (Tailgaterz, 3.3 x 2.7 x 2.0 m), pitched outside (**Supplementary Material: Fig. S3**) and containing 5 hummingbird feeders in syringe- and bottle-form. To identify any harness-induced entanglement [44], we also ensured that

the tent contained numerous shrubs and large branches, which doubled as both perches and flight obstacles.

In the case of the 1-hour trials, we monitored individuals continuously to verify active flight within the tent without ensnarement; when conducting overnight trials, we ensured that all birds were acclimated to the tent at least one hour prior to sunset, then monitored individuals until they successfully fed from the feeders, and then once every hour until sunset. Once we had determined that the bird had fallen asleep, we left it undisturbed until early morning, as hummingbirds are inactive at night [66,67]. We then inspected the bird for any signs of harness-induced abrasion or chafing, removed the backpack harness, weighed the individual, and released it—except in the case of a single, extended trial that we ran for 24 hours (as a supplemental check against any longer-term effects), wherein we resumed hourly checks until an early afternoon release. In all cases, we monitored individuals from afar (with the occasional aid of binoculars) to reduce their stress levels. At the end of each trial, we recaptured the bird from the enclosure for release. Given how critical predator evasion is for potential prey organisms, we considered a hummingbird’s flight performance unimpaired [22] if each tagged bird could successfully evade us (a proxy for predators) for over 60 seconds without becoming entangled. As these trials were purely observational with a binary outcome (successful free flight or ensnarement), we did not conduct a statistical analysis on this component of the study.

Results

Time-budget summaries and tag effects.

We had two cases of acclimation failure, in which one bird failed to feed from the syringe and a second failed to locate and rest upon the perch; subsequently, both individuals displayed signs of distress in the first 30 minutes of the trial. As such, we did not include either bird in our dataset (although we note that neither suffered lasting distress, and flew away vigorously upon their immediate release). With 25 successful trials each containing two 1-hour video-recorded observation periods, our complete dataset comprised 50 total hummingbird observation hours. Over the course of each 3-hour trial, individual hummingbirds drank an average of 3.65 ± 1.62 grams of sugar water from the syringe—nearly half their body mass. From start to finish, the birds themselves experienced mass changes ranging from a loss of 1.13 grams to a gain of 1.82 grams; their average change in mass, however, was an increase of 0.48 grams (standard deviation ± 0.59 grams). In no cases did the hummingbirds’ flight patterns, standard forward flight or hovering alike, appear impeded by the addition of the radio-transmitter backpack harness.

The proportion of the treatment period that individuals spent conducting each behavior differed depending on whether the bird was tagged or not (**Table 2, Fig. 2**): when tagged, individuals spent on average 3.46% less time flying, 0.19% more time hover-feeding, 1.48% more time preening, and 1.78% more time perching without preening. As can be seen here, favoring perching over flying did not exclude the concomitant possibility of more hover-feeding, given that birds’ brief flights transitioning between the perch and syringe constituted a nominal proportion of overall time budgets. In **Tables 3 and 4**, we present the average number of times individuals flew, fed, preened, and perched in each treatment (number of “bouts”), and the lengths of those bouts, respectively. When tagged, birds had, on average, 23 fewer flight bouts that averaged 0.57 seconds shorter, 1

less hover-feeding bout that averaged 0.53 seconds longer, 12 more preening bouts that averaged 0.69 seconds longer, and 24 fewer perching bouts that averaged 268.2 seconds longer than when untagged.

Model selection.

We present all our model-ranking results, each of which accounted for the random effect of individual, in **Table 5**, and the parameter summaries of our top-supported models in **Supplementary Material: Table S2**. For time spent flying, the best-supported model included the additive effects of randomized treatment type and treatment number (**Fig. 3A**). Though the effect of whether the bird was tagged or not did not significantly improve model fit (95% CI = -6.72 – 305.49; $p = 0.070$), individuals flew, on average, for 25.54% of their tagged treatment and 29.00% of their untagged treatment. On the other hand, individuals averaged 23.95% of their first treatment flying, and later 30.59% in their second—a significant increase of 6.64% (95% CI = 62.64 – 374.84; $p = 0.011$). Three additional flight duration models, incorporating the following additive effects, exhibited a competitive ranking (within 2 ΔAICc of the top model): **(1)** treatment number, treatment type, and bird mass; **(2)** treatment number only; and **(3)** treatment number, treatment type, bird mass, and nectar concentration. However, we found that the additional parameters in these more complex models had only modest effects.

For feeding duration, the best-supported model included only a single fixed effect: bird mass (**Fig. 3B**). In general, lighter birds fed significantly more (95% CI = -0.51 – -0.07; $p = 0.011$). No other models were competitive (the null model was second-best, with a ΔAICc of 7.62). With individuals hover-feeding for an average of 1.15% of their tagged treatment and 0.96% of their untagged treatment, treatment type was not included in the top-performing model.

For time spent preening, meanwhile, the best-supported model included the additive effects of treatment type and the period of day when the treatment took place (**Fig 3C**). Here, the effect of treatment type significantly improved model fit (95% CI = -2.36 – -0.39; $p = 0.011$); individuals preened for an average of 1.97% and 0.49% of their tagged and untagged treatments, respectively. As the day went on, the birds spent progressively more time preening: on average, birds spent 0.24% of their treatments preening when they occurred in the morning, 1.19% when they were in the afternoon, and 3.81% in the evening. This constituted a significant, 0.96% increase from morning to afternoon (95% CI = -3.17 – -0.80; $p = 0.002$), and a 2.62% (non-significant) increase from afternoon to evening (95% CI = -0.36 – 1.81; $p = 0.192$). In the case of preening models, only one other model incorporating the additive effects of treatment type, period of day, and nectar concentration had a competitive ranking; similarly with the flight models described above, the additional parameter of concentration only had a modest effect.

Inter-rater reliability.

With 6 raters scoring the same 4 videos, our single-score intraclass correlation coefficient was 0.998 (95% CI = 0.996 – 0.999; $p = 4.08\text{e-}97$). This coefficient exceeds the 0.80 threshold specified by Gwet [68] and fulfills “excellent” consistency standards, suggesting a well-defined ethogram and little ambiguity in our behavioral categories [59].

Entanglement experiment.

In all Entanglement Experiment trials, the hummingbirds flew, perched, fed, preened, and slept without getting entangled in vegetation, including during our recapture efforts, nor did they show any signs of distress [51]. Our overnight trials lasted from 15.4–24 hours (average of 18.57 ± 3.06 hours). Similarly to the Behavior Experiment, there were no perceptible tag effects; the birds appeared to fly without issue. With a more spacious, natural environment than in the Behavior Experiment, the hummingbirds were less constrained and could perform longer forward flights, as well as explore their surroundings to a greater degree. To this end, the birds appeared visibly calmer, perching and feeding more readily than their Behavior-Experiment counterparts. We had no cases of acclimation failure in these tests, nor did we observe any signs of harness-induced chafing or abrasions.

Discussion

Behavior experiment.

Our work provides a straightforward experimental design for field-accessible biologging ethics—randomized, tagged and untagged treatments that incorporate both acclimation and video-recording periods for subsequent time-budget breakdowns—which can be reproduced with numerous taxa, particularly small avian species. To our knowledge, this is the first investigation to combine the use of multiple biologgers (RFID tags and radio-transmitters) to the study of hummingbirds. The collective mass of these two tags averaged 5.93% of our tested Black-throated Mangoes' body masses (**Table 1**). While exceeding the 5% standard intended for deployments in the wild [69], we note that hummingbirds, on account of their small size, have a higher strength-to-bodyweight ratio than larger birds and are therefore proportionally stronger [70–72] (yet this is not to say that they would be unaffected by potential aerodynamic changes induced by biologgers). Although individuals behaved according to our predictions when equipped with radio-tag backpack harnesses (on average flying less, but hover-feeding, preening, and perching more), this difference was only statistically significant in the case of preening. The effect of tagging was included in the best-supported models for both flying and preening duration (which also included the additive effects of treatment number and period of day, respectively), while the best-supported model for feeding duration included only bird mass.

The impact of radio-transmitters on flight duration demonstrated here is consistent with findings that Ruby-throated Hummingbirds spend up to 11% less time flying when outfitted with a variety of radio-tags [28], although in our case the difference was less pronounced (in this experiment, individuals averaged 3.46% less time flying when tagged). Along these lines, the effect of tagging was non-significant in our model, in contrast to treatment number: birds flew significantly more in their second treatment. It is possible that, as the birds became more accustomed to the enclosure (reduced neophobia), they grew more comfortable exploring [73]; research has shown that “approach latency” (the speeds at which animals approach novelty) can vary between avian species [74]. A more likely explanation is that the hummingbirds experienced increasing stress as the trials went on. This could be due to additional time in captivity—chronic stress experiments have demonstrated that corticosterone and daytime activity levels can steadily increase to peak in birds after multiple days in captivity [75], although we did not observe any signs of undue distress (as outlined by Russell et al. [51]) in our video analyses. Furthermore, the acute stress of being

captured, handled, and processed twice in relatively quick succession may have increased individuals' agitation [76–78], compelling them to remain in a high-alert state throughout their second treatment.

The effect of tagging did not factor into the best-supported model for feeding duration; individuals only spent an average of 0.19% more time feeding when tagged. Regarding the significant effect of bird mass in our top model, it is likely that the lighter hummingbirds that we tested had smaller energy reserves (e.g., body fat, nectar in their crop or digestive system) and maximized their short-term energy intake via the undefended resource provided in the experiment [79–81]. This would allow them to better accumulate fat [82] and reduce the need for risky torpor [83]. Pre-trial, individuals differed among themselves by up to 24% in body mass (7.12–9.31 grams), and over the course of the experiment consumed vastly different quantities of nectar—as little as 3.7% (0.28 grams by a 7.48-gram bird) and as much as 85% (6.62 grams by a 7.77-gram bird) of total body mass.

In contrast to the other behaviors, the effect of tagging was significant in our best-supported preening model, with individuals spending, on average, 1.48% more time preening while tagged. This increase is not surprising given the established link between preening and externally fitted biologgers [45–47], suggesting that radio-tagged hummingbirds will similarly expend more energy attempting to physically remove the harness and/or tag from their bodies. More unexpected, meanwhile, was the effect of period of day in our top model. Birds preened significantly more in the afternoon than in the morning (an average increase of 0.96%), and more in the evening than in the afternoon (a non-significant average increase of 2.62%). The reasoning for this relationship is less clear. Reported trends in hummingbird activity as they relate to time of day are somewhat conflicting, with some studies suggesting that feeding activity—which will detract from possible preening time—peaks in morning and evening [84], and others demonstrating steady decreases in feeding activity throughout the day, specifically in the case of *ad libitum* nectar provision [85,86]. Yet there is little information regarding how time spent preening relates to time of day, and further study is warranted. Zenzal et al. [28] point out that birds equipped with auxiliary markers of any kind will exhibit temporary increases in preening levels before resuming habitual behavior; our results suggest that prolonged monitoring can help to explore circadian effects on time budgets, especially as they relate to biologging ethics.

Entanglement experiment.

Our research procedure also enabled us to explore the safety of our backpack harness design. As biologger attachment design can play a major role in tag-induced entanglement and mortality [44], we focused on an observational approach to reflect (as closely as possible) routine hummingbird behavior while in an aviary-like setting. Here, we found that no Black-throated Mangoes suffered vegetative entanglement—even during our recapture efforts at the end of each trial, which we considered a proxy for their ability to evade large predators—nor did we observe any negative effects from overnight wear. See **Supplementary Material: Harness and Device Chassis Design** for a discussion of this particular harness' limitations and risks with respect to other hummingbird species that we tested in our pilot study.

Limitations and future directions.

We currently lack the tools to continuously monitor the behavior of free-living (uncaptured) hummingbirds [87], particularly in ways that will enable comparison between tagged and untagged individuals (e.g., individuals to act as controls against birds equipped with accelerometers). Rigorous studies of hummingbird biologging ethics must therefore be conducted in confined settings, yet captivity can have significant effects on avian behavior [88,89]; we advise caution when extrapolating our results to entirely wild studies [28]. Although our entanglement enclosure was more reflective of a hummingbird's everyday habitat and may have allowed for more "natural" behavior, outdoor filming would have posed both logistical (e.g., camera exposure to rain and humidity [90,91]) and analytical (e.g., visually identifying hummingbirds against non-uniform or low-contrast backgrounds [92,93]) challenges. Even in an indoor setting, we found the video-analysis stage to be painstaking, owing to the majority of birds undertaking hundreds of rapid flights in each 1-hour treatment (an average of 339 ± 230 when tagged and 362 ± 241 when untagged), as well as due to software-related issues (e.g., BORIS crashing often).

Longer-term biologging experiments, on the other hand, would allow for a much more comprehensive examination of both behavior and harness-induced issues. The first several hours (and days) in captivity are a critical period of adjustment for birds, in which stress can be so acute as to result in mortality [94,95]. Although birds in our experiment had perching rates comparable to those reported in partial time budget observations conducted in the wild [31,96], and we incorporated a much longer acclimation and observation window than in similar studies [28], lengthening these periods even further may allow for results that more meaningfully reflect natural hummingbird behavior. A longer experiment would additionally allow for both a more realistic examination of any device-induced skin abrasion (which may only be evident after prolonged exposure) and, in an aviary setting, the likelihood of vegetative entanglement (especially after the prolonged energetic cost of bearing a biologger, which can exhaust animals over time [97]). Of course, beyond the scope of captivity, capture-recapture studies would allow for an estimation of free-living survival rates associated with this attachment method [11].

In general, follow-up studies could take a multitude of valuable directions. Incorporating additional aspects of hummingbird biology beyond behavior—such as kinematic and biomechanical compensation for additional weight load through the use of wind tunnels or high-speed cameras [6,23,30,98], or maneuverability via flight-trajectory tracking within enclosures [99]—would help address other pressing concerns, including escape response speeds and accelerations as proxies for survivability [100]. We also elected to sample only males, given that we had no plans to deploy such potentially long-term (harnessed) 5.5% bodyweight tags on females, which already bear the substantial weight of developing eggs during nesting seasons [37]. However, given the possibility of sex-specific impacts of biologgers [101,102], future studies would benefit from working with female hummingbirds as well. Finally, high-quality labelled time budget datasets, such as the one produced through this study (which has a consistent background and focal organism, and starkly differentiated behaviors), would provide necessary training and testing data for machine learning algorithms in identifying animal behaviors, opening the door to fresh advancements between ecology and computer vision alike [103].

Conclusions

Our research approach allowed us to compare the time budgets of captive Black-throated Mangoes when they were and were not equipped with radio-transmitter backpack harnesses. While we found that hummingbirds overall flew less, but perched, hover-fed, and preened more when tagged (in addition to adjusting the number of bouts and bout durations of these different behaviors), this difference was only statistically significant in the case of preening. Through our mixed-effects modeling, we characterized the effects of tagging and additional variables on how long hummingbirds conducted these behaviors. We found that the top-supported model for flight included the additive effects of treatment type and treatment number (a significant effect), while feeding's top model included only bird mass (a significant effect), and the best-supported model for perching included the additive effects of treatment type and period of day (both significant effects). Our tests are fairly straightforward to replicate and/or adjust depending on species-specific needs, providing remote- and field-accessible methodology that can be applied more broadly as a pre-release checkpoint when tagging small-bodied birds—a sorely needed addition to the field of biologging ethics. With that said, we advise caution when interpreting the findings of this study beyond the scope of captive experiments.

Abbreviations

- **RFID:** radio-frequency identification
- **BORIS:** Behavioral Observation Research Interactive Software
- **AICc:** Akaike's information criterion corrected for small sample sizes

Declarations

Ethics approval and consent to participate.

We conducted all work under the approval of the University of Washington's Institutional Animal Care and Use Committee (IACUC protocol number: 4498-05), and our research permit was issued by Corporación Autónoma Regional de Cundinamarca (permit number: 50227001473). All Ecuadorian pilot research was conducted under the approval and permission of Ministerio del Ambiente y Agua (permit ID: MAAE-ARSFC-2021-1126).

Consent for publication.

Not applicable.

Availability of data and materials.

The datasets and code generated from our study are available in the Dryad repository, at the following link: <https://datadryad.org/dataset/doi:10.5061/dryad.44j0zpcqw>.

Competing interests.

The authors declare that they have no competing interests.

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Authors' contributions.

Lead author AJS led the investigation, project administration, validation, visualization, statistical analysis, figure/table preparation, and writing all drafts of the manuscript; senior author ARG led supervision efforts, and co-led project conceptualization and funding acquisition efforts alongside AJS. AJS, ARG, AMF, and RE established methodology; YT led custom chassis design efforts alongside AJS. Fieldwork was conducted by AJS, AMF, MAM, NTC, and NB. AJS, AMF, and YT led data curation, and all video processing was conducted by AJS, AMF, AEC, SGM, LH, ANC, YS, OAC, and MCF. All authors read, provided feedback for, and approved the final manuscript.

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References

1. Kays R, Crofoot MC, Jetz W, Wikelski M. Terrestrial animal tracking as an eye on life and planet. *Science*. American Association for the Advancement of Science; 2015;348:aaa2478. <https://doi.org/10.1126/science.aaa2478>
2. Kay WP, Naumann DS, Bowen HJ, Withers SJ, Evans BJ, Wilson RP, et al. Minimizing the impact of biologging devices: Using computational fluid dynamics for optimizing tag design and positioning. *Methods Ecol Evol*. 2019;10:1222–33. <https://doi.org/10.1111/2041-210X.13216>
3. Wilson RP, McMahon CR. Measuring devices on wild animals: what constitutes acceptable practice? *Front Ecol Environ*. 2006;4:147–54. [https://doi.org/10.1890/1540-9295\(2006\)004\[0147:MDOWAW\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2006)004[0147:MDOWAW]2.0.CO;2)
4. Vandenabeele S, Wilson R, Grogan A. Tags on seabirds: How seriously are instrument-induced behaviours considered? *Anim Welf South Mimms Engl*. 2011;20:559–71.
5. Authier M, Péron C, Mante A, Vidal P, Grémillet D. Designing observational biologging studies to assess the causal effect of instrumentation. *Methods Ecol Evol*. 2013;4:802–10. <https://doi.org/10.1111/2041-210X.12075>

6. Mizrahy-Rewald O, Winkler N, Amann F, Neugebauer K, Voelkl B, Grogger HA, et al. The impact of shape and attachment position of biologging devices in Northern Bald Ibises. *Anim Biotelemetry*. 2023;11:8. <https://doi.org/10.1186/s40317-023-00322-5>
7. Arrondo E, Pérez-García JM. Call for a critical review of widespread use of animal tracking devices. *Eur J Wildl Res*. 2025;71:27. <https://doi.org/10.1007/s10344-025-01906-7>
8. Kölzsch A, Neefjes M, Barkway J, Müskens GJDM, van Langevelde F, de Boer WF, et al. Neckband or backpack? Differences in tag design and their effects on GPS/accelerometer tracking results in large waterbirds. *Anim Biotelemetry*. 2016;4:13. <https://doi.org/10.1186/s40317-016-0104-9>
9. Fritz J, Eberhard B, Esterer C, Goenner B, Trobe D, Unsoeld M, et al. Biologging is suspect to cause corneal opacity in two populations of wild living Northern Bald Ibises (*Geronticus eremita*). *Avian Res*. 2020;11:38. <https://doi.org/10.1186/s40657-020-00223-8>
10. Paredes R, Jones IL, Boness DJ. Reduced parental care, compensatory behaviour and reproductive costs of thick-billed murre equipped with data loggers. *Anim Behav*. 2005;69:197–208. <https://doi.org/10.1016/j.anbehav.2003.12.029>
11. Barron DG, Brawn JD, Weatherhead PJ. Meta-analysis of transmitter effects on avian behaviour and ecology. *Methods Ecol Evol*. 2010;1:180–7. <https://doi.org/10.1111/j.2041-210X.2010.00013.x>
12. Bodey TW, Cleasby IR, Bell F, Parr N, Schultz A, Votier SC, et al. A phylogenetically controlled meta-analysis of biologging device effects on birds: Deleterious effects and a call for more standardized reporting of study data. *Methods Ecol Evol*. 2018;9:946–55. <https://doi.org/10.1111/2041-210X.12934>
13. Dennis TE, Shah SF. Assessing Acute Effects of Trapping, Handling, and Tagging on the Behavior of Wildlife Using GPS Telemetry: A Case Study of the Common Brushtail Possum. *J Appl Anim Welf Sci*. Routledge; 2012;15:189–207. <https://doi.org/10.1080/10888705.2012.683755>
14. Godfrey JD, Bryant DM, Williams MJ. Radio-telemetry increases free-living energy costs in the endangered Takahe *Porphyrio mantelli*. *Biol Conserv*. 2003;114:35–8. [https://doi.org/10.1016/S0006-3207\(02\)00416-0](https://doi.org/10.1016/S0006-3207(02)00416-0)
15. Bowlin MS, Henningsson P, Muijres FT, Vleugels RHE, Liechti F, Hedenström A. The effects of geolocator drag and weight on the flight ranges of small migrants. *Methods Ecol Evol*. 2010;1:398–402. <https://doi.org/10.1111/j.2041-210X.2010.00043.x>
16. Tomotani BM, Bil W, van der Jeugd HP, Pieters RPM, Muijres FT. Carrying a logger reduces escape flight speed in a passerine bird, but relative logger mass may be a misleading measure of this flight performance detriment. *Methods Ecol Evol*. 2019;10:70–9. <https://doi.org/10.1111/2041-210X.13112>
17. Wilson RP, Grémillet D, Syder J, Kierspel MAM, Garthe S, Weimerskirch H, et al. Remote-sensing systems and seabirds: their use, abuse and potential for measuring marine environmental variables. *Mar Ecol Prog Ser*. 2002;228:241–61. <https://doi.org/10.3354/meps228241>
18. Phillips RA, Xavier JC, Croxall JP. Effects of Satellite Transmitters on Albatrosses and Petrels. *The Auk*. 2003;120:1082–90. <https://doi.org/10.1093/auk/120.4.1082>
19. Portugal SJ, White CR. Miniaturization of biologgers is not alleviating the 5% rule. *Methods Ecol Evol*. 2018;9:1662–6. <https://doi.org/10.1111/2041-210X.13013>
20. Caccamise DF, Hedin RS. An Aerodynamic Basis for Selecting Transmitter Loads in Birds. *Wilson Bull. Wilson Ornithological Society*; 1985;97:306–18.

21. Casper RM. Guidelines for the instrumentation of wild birds and mammals. *Anim Behav.* 2009;78:1477–83. <https://doi.org/10.1016/j.anbehav.2009.09.023>
22. Lind J, Jakobsson S, Kullberg C. Impaired Predator Evasion in the Life History of Birds: Behavioral and Physiological Adaptations to Reduced Flight Ability. In: Thompson CF, editor. *Curr Ornithol Vol 17* [Internet]. New York, NY: Springer; 2010 [cited 2023 May 10]. p. 1–30. https://doi.org/10.1007/978-1-4419-6421-2_1
23. Altshuler DL, Dudley R. Kinematics of hovering hummingbird flight along simulated and natural elevational gradients. *J Exp Biol.* 2003;206:3139–47. <https://doi.org/10.1242/jeb.00540>
24. Kou G, Wang Y, Dudley R, Wu Y, Li D. Coping with captivity: takeoff speed and load-lifting capacity are unaffected by substantial changes in body condition for a passerine bird. *J Exp Biol.* 2022;225:jeb244642. <https://doi.org/10.1242/jeb.244642>
25. Pennycuick CJ, Fuller MR, McALLISTER L. Climbing Performance of Harris’ Hawks (*Parabuteo unicinctus*) With Added Load: Implications for Muscle Mechanics and for Radiotracking. *J Exp Biol.* 1989;142:17–29. <https://doi.org/10.1242/jeb.142.1.17>
26. Longarini A, Duriez O, Shepard E, Safi K, Wikelski M, Scacco M. Effect of harness design for tag attachment on the flight performance of five soaring species. *Mov Ecol.* 2023;11:39. <https://doi.org/10.1186/s40462-023-00408-y>
27. Vandenabeele SP, Grundy E, Friswell MI, Grogan A, Votier SC, Wilson RP. Excess Baggage for Birds: Inappropriate Placement of Tags on Gannets Changes Flight Patterns. *PLOS ONE.* Public Library of Science; 2014;9:e92657. <https://doi.org/10.1371/journal.pone.0092657>
28. Zenzal TJ Jr, Diehl RH, Moore FR. The impact of radio-tags on Ruby-throated Hummingbirds (*Archilochus colubris*). *The Condor.* 2014;116:518–26. <https://doi.org/10.1650/CONDOR-13-142.1>
29. Culik BM, Pütz K, Wilson RP, Allers D, Lage J, Bost CA, et al. Diving energetics in king penguins (*Aptenodytes patagonicus*). *J Exp Biol.* 1996;199:973–83. <https://doi.org/10.1242/jeb.199.4.973>
30. Vandenabeele SP, Shepard ELC, Grémillet D, Butler PJ, Martin GR, Wilson RP. Are bio-telemetric devices a drag? Effects of external tags on the diving behaviour of great cormorants. *Mar Ecol Prog Ser.* 2015;519:239–49. <https://doi.org/10.3354/meps11058>
31. Wolf LL, Hainsworth FR. Time and Energy Budgets of Territorial Hummingbirds. *Ecology.* 1971;52:980–8. <https://doi.org/10.2307/1933803>
32. Suarez RK. Hummingbird flight: Sustaining the highest mass-specific metabolic rates among vertebrates. *Experientia.* 1992;48:565–70. <https://doi.org/10.1007/BF01920240>
33. Shankar A, Powers DR, Dávalos LM, Graham CH. The allometry of daily energy expenditure in hummingbirds: An energy budget approach. *J Anim Ecol.* 2020;89:1254–61. <https://doi.org/10.1111/1365-2656.13185>
34. Chai P, Millard D. Flight and size constraints: hovering performance of large hummingbirds under maximal loading. *J Exp Biol.* The Company of Biologists Ltd; 1997;200:2757–63.
35. Falk JJ, Rubenstein DR, Rico-Guevara A, Webster MS. Intersexual social dominance mimicry drives female hummingbird polymorphism. *Proc R Soc B Biol Sci. Royal Society;* 2022;289:20220332. <https://doi.org/10.1098/rspb.2022.0332>
36. Ortega-Jimenez VM, Badger M, Wang H, Dudley R. Into rude air: hummingbird flight performance in variable aerial environments. *Philos Trans R Soc B Biol Sci. Royal Society;* 2016;371:20150387. <https://doi.org/10.1098/rstb.2015.0387>

37. Fierro-Calderón K, Martin TE. Reproductive Biology of the Violet-Chested Hummingbird in Venezuela and Comparisons with Other Tropical and Temperate Hummingbirds. *The Condor*. 2007;109:680–5. <https://doi.org/10.1093/condor/109.3.680>
38. Hadley AS, Betts MG. Tropical deforestation alters hummingbird movement patterns. *Biol Lett*. 2009;5:207–10. <https://doi.org/10.1098/rsbl.2008.0691>
39. Williamson JL, Witt CC. A lightweight backpack harness for tracking hummingbirds. *J Avian Biol* [Internet]. 2021 [cited 2022 Oct 31];52. <https://doi.org/10.1111/jav.02802>
40. Sargent AJ, Groom DJE, Rico-Guevara A. Locomotion and Energetics of Divergent Foraging Strategies in Hummingbirds: A Review. *Integr Comp Biol*. 2021;61:736–48. <https://doi.org/10.1093/icb/icab124>
41. Rueda-Urbe C, Sargent AJ, Echeverry-Galvis MÁ, Camargo-Martínez PA, Capellini I, Lancaster LT, et al. Tracking Small Animals in Complex Landscapes: A Comparison of Localisation Workflows for Automated Radio Telemetry Systems. *Ecol Evol*. 2024;14:e70405. <https://doi.org/10.1002/ece3.70405>
42. Bandivadekar RR, Pandit PS, Sollmann R, Thomas MJ, Logan SM, Brown JC, et al. Use of RFID technology to characterize feeder visitations and contact network of hummingbirds in urban habitats. *PLOS ONE*. Public Library of Science; 2018;13:e0208057. <https://doi.org/10.1371/journal.pone.0208057>
43. Falk JJ, Webster MS, Rubenstein DR. Male-like ornamentation in female hummingbirds results from social harassment rather than sexual selection. *Curr Biol*. 2021;31:4381–4387.e6. <https://doi.org/10.1016/j.cub.2021.07.043>
44. Dougill SJ, Johnson L, Banko PC, Goltz DM, Wiley MR, Semones JD. Consequences of antenna design in telemetry studies of small passerines. *J Field Ornithol*. Association of Field Ornithologists; 2000;71:385–8. <https://doi.org/10.1648/0273-8570-71.3.385>
45. Robert M, Drolet B, Savard J-PL. Effects of Backpack Radio-Transmitters on Female Barrow's Goldeneyes. *Waterbirds*. The Waterbird Society; 2006;29:115–20. [https://doi.org/10.1675/1524-4695\(2006\)29\[115:EOBROF\]2.0.CO;2](https://doi.org/10.1675/1524-4695(2006)29[115:EOBROF]2.0.CO;2)
46. Booms TL, Schempf PF, Fuller MR. Preening Behavior of Adult Gyrfalcons Tagged with Backpack Transmitters. *J Raptor Res*. Raptor Research Foundation; 2011;45:264–7. <https://doi.org/10.3356/JRR-10-115.1>
47. Herrod A, King M, Ingwersen D, Clarke RH. Tracking devices attached with harnesses influence behaviour but not body mass of Princess Parrots *Polytelis alexandrae*. *J Ornithol*. 2014;155:519–29. <https://doi.org/10.1007/s10336-013-1034-4>
48. Quesnel VC, Quesnel VC. The case history of an aberrant Black-throated Mango hummingbird *Anthracothonax nigricollis*. *Bull Br Ornithol Club*. 1995;115:25--27.
49. Rochford M. Nesting Behaviour by a Male Plumaged Black-throated Mango Hummingbird, *Anthracothonax nigricollis nigricollis*. *Living World J Trinidad Tobago Field Nat Club* [Internet]. 2012 [cited 2024 Apr 24]; <https://ttfnc.org/livingworld/index.php/lwj/article/view/rochford2012>. Accessed 24 Apr 2024
50. Diamant ES, Falk JJ, Rubenstein DR. Male-like female morphs in hummingbirds: the evolution of a widespread sex-limited plumage polymorphism. *Proc R Soc B Biol Sci*. Royal Society; 2021;288:20203004. <https://doi.org/10.1098/rspb.2020.3004>
51. Russell SM, Russell RO, Pollock J, Hill A. *The North American Banders' Manual for Hummingbirds* [Internet]. Point Reyes Station, California, USA; 2019.

- efaidnbmnnnibpcajpcglclefindmkaj/https://www.nabanding.net/wp-content/uploads/2019/11/Hummingbird-Manual-31_Oct_2019.pdf
52. Tell LA, Hazlehurst JA, Bandivadekar RR, Brown JC, Spence AR, Powers DR, et al. Hummingbird (family Trochilidae) research: welfare-conscious study techniques for live hummingbirds and processing of hummingbird specimens. Museum of Texas Tech University; 2021.
 53. English SG, Wilson S, Bandivadekar RR, Graves EE, Holyoak M, Brown JC, et al. Quantifying phenology and migratory behaviours of hummingbirds using single-site dynamics and mark-detection analyses. *Proc R Soc B Biol Sci. Royal Society*; 2022;289:20220991. <https://doi.org/10.1098/rspb.2022.0991>
 54. Brewer LW, Redmond CA, Stafford JM, Hatch GE. Marking ruby-throated hummingbirds with radio frequency identification tags. *J Wildl Manag.* 2011;75:1664–7. <https://doi.org/10.1002/jwmg.222>
 55. Hou L, Verdirame M, Welch KC. Automated tracking of wild hummingbird mass and energetics over multiple time scales using radio frequency identification (RFID) technology. *J Avian Biol.* 2015;46:1–8. <https://doi.org/10.1111/jav.00478>
 56. BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations - Friard - 2016 - *Methods in Ecology and Evolution* - Wiley Online Library [Internet]. [cited 2022 Nov 2]. <https://besjournals.onlinelibrary.wiley.com/doi/full/10.1111/2041-210X.12584>. Accessed 2 Nov 2022
 57. R Core Team. R: A language and environment for statistical computing. [Internet]. Vienna, Austria; 2023. <https://www.R-project.org/>.
 58. Gamer M, Lemon J, Singh IFP. irr: Various Coefficients of Interrater Reliability and Agreement [Internet]. 2019 [cited 2025 Jan 28]. <https://cran.r-project.org/web/packages/irr/index.html>. Accessed 28 Jan 2025
 59. Harvey ND. A Simple Guide to Inter-rater, Intra-rater and Test-retest Reliability for Animal Behaviour Studies. *OSF*; 2024 [cited 2024 Jan 1]; <https://doi.org/10.31219/osf.io/8stpy>
 60. Bates D, Maechler M, Bolker B, Walker S, Christensen RHB, Singmann H, et al. lme4: Linear Mixed-Effects Models using “Eigen” and S4 [Internet]. 2022 [cited 2022 Nov 6]. <https://CRAN.R-project.org/package=lme4>. Accessed 6 Nov 2022
 61. Kuznetsova A, Brockhoff PB, Christensen RHB. lmerTest Package: Tests in Linear Mixed Effects Models. *J Stat Softw.* 2017;82. <https://doi.org/10.18637/jss.v082.i13>
 62. Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, et al. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J. Technische Universitaet Wien*; 2017;9:378–400. <https://doi.org/10.3929/ethz-b-000240890>
 63. Hartig F, Lohse L, leite M de S. DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models [Internet]. 2024 [cited 2025 Jan 28]. <https://cran.r-project.org/web/packages/DHARMA/index.html>. Accessed 28 Jan 2025
 64. Benjamini Y, Hochberg Y. Controlling the False Discovery Rate: A Practical and Powerful Approach to Multiple Testing. *J R Stat Soc Ser B Methodol.* 1995;57:289–300. <https://doi.org/10.1111/j.2517-6161.1995.tb02031.x>
 65. Eckert SA, Jesper AC. Home range, site fidelity, and movements of timber rattlesnakes (*Crotalus horridus*) in west-central Illinois. *Anim Biotelemetry.* 2024;12:1. <https://doi.org/10.1186/s40317-023-00357-8>

66. Wagner HO. Food and Feeding Habits of Mexican Hummingbirds. Wilson Bull. Wilson Ornithological Society; 1946;58:69–93.
67. Shankar A, Cisneros INH, Thompson S, Graham CH, Powers DR. A heterothermic spectrum in hummingbirds. J Exp Biol. 2022;225:jeb243208. <https://doi.org/10.1242/jeb.243208>
68. Gwet KL. Handbook of Inter-Rater Reliability, 4th Edition: The Definitive Guide to Measuring The Extent of Agreement Among Raters. Advanced Analytics, LLC; 2014.
69. Naef-Daenzer B, Widmer F, Nuber M. A test for effects of radio-tagged on survival and movements of small birds. Avian Sci. 2001;1:15–23.
70. Cheng B, Tobalske BW, Powers DR, Hedrick TL, Wang Y, Wethington SM, et al. Flight mechanics and control of escape manoeuvres in hummingbirds. II. Aerodynamic force production, flight control and performance limitations. J Exp Biol. 2016;219:3532–43. <https://doi.org/10.1242/jeb.137570>
71. Chin DD, Lentink D. Flapping wing aerodynamics: from insects to vertebrates. J Exp Biol. 2016;219:920–32. <https://doi.org/10.1242/jeb.042317>
72. Agrawal S, Tobalske BW, Anwar Z, Luo H, Hedrick TL, Cheng B. Musculoskeletal wing-actuation model of hummingbirds predicts diverse effects of primary flight muscles in hovering flight. Proc R Soc B Biol Sci. Royal Society; 2022;289:20222076. <https://doi.org/10.1098/rspb.2022.2076>
73. Greggor AL, Jolles JW, Thornton A, Clayton NS. Seasonal changes in neophobia and its consistency in rooks: the effect of novelty type and dominance position. Anim Behav. 2016;121:11–20. <https://doi.org/10.1016/j.anbehav.2016.08.010>
74. O'Hara M, Mioduszevska B, von Bayern A, Auersperg A, Bugnyar T, Wilkinson A, et al. The temporal dependence of exploration on neotic style in birds. Sci Rep. Nature Publishing Group; 2017;7:4742. <https://doi.org/10.1038/s41598-017-04751-0>
75. Fischer CP, Wright-Lichter J, Romero LM. Chronic stress and the introduction to captivity: How wild house sparrows (*Passer domesticus*) adjust to laboratory conditions. Gen Comp Endocrinol. 2018;259:85–92. <https://doi.org/10.1016/j.ygcen.2017.11.007>
76. Omsjoe EH, Stien A, Irvine J, Albon SD, Dahl E, Thoresen SI, et al. Evaluating capture stress and its effects on reproductive success in Svalbard reindeer. Can J Zool. NRC Research Press; 2009;87:73–85. <https://doi.org/10.1139/Z08-139>
77. Harcourt RG, Turner E, Hall A, Waas JR, Hindell M. Effects of capture stress on free-ranging, reproductively active male Weddell seals. J Comp Physiol A. 2010;196:147–54. <https://doi.org/10.1007/s00359-009-0501-0>
78. Fernández-Morán J, Saavedra D, Torre JRDL, Manteca-Vilanova X. Stress in wild-caught Eurasian otters (*Lutra lutra*): effects of a long-acting neuroleptic and time in captivity. Anim Welf. 2004;13:143–9. <https://doi.org/10.1017/S0962728600026889>
79. Hainsworth FR, Tardiff MF, Wolf LL. Proportional Control for Daily Energy Regulation in Hummingbirds. Physiol Zool. [University of Chicago Press, Division of Comparative Physiology and Biochemistry, Society for Integrative and Comparative Biology]; 1981;54:452–62.
80. Carpenter FL, Hixon MA, Hunt A, Russell RW. Why hummingbirds have such large crops. Evol Ecol. 1991;5:405–14. <https://doi.org/10.1007/BF02214157>
81. Eberts ER, Dick MF, Welch KC. Metabolic Fates of Evening Crop-Stored Sugar in Ruby-Throated Hummingbirds (*Archilochus colubris*). Diversity. Multidisciplinary Digital Publishing Institute; 2019;11:9. <https://doi.org/10.3390/d11010009>

82. Powers DR, Brown AR, Van Hook JA. Influence of Normal Daytime Fat Deposition on Laboratory Measurements of Torpor Use in Territorial versus Nonterritorial Hummingbirds. *Physiol Biochem Zool.* The University of Chicago Press; 2003;76:389–97. <https://doi.org/10.1086/374286>
83. Shankar A, Schroeder RJ, Wethington SM, Graham CH, Powers DR. Hummingbird torpor in context: duration, more than temperature, is the key to nighttime energy savings. *J Avian Biol* [Internet]. 2020 [cited 2022 Nov 3];51. <https://doi.org/10.1111/jav.02305>
84. Stiles FG, Wolf LL. Hummingbird Territoriality at a Tropical Flowering Tree. *The Auk.* American Ornithological Society; 1970;87:467–91. <https://doi.org/10.2307/4083791>
85. Powers DR, McKee T. The Effect of Food Availability on Time and Energy Expenditures of Territorial and Non-Territorial Hummingbirds. *The Condor.* American Ornithological Society; 1994;96:1064–75. <https://doi.org/10.2307/1369115>
86. Gass CL, Garrison JSE. Energy regulation by traplining hummingbirds. *Funct Ecol.* 1999;13:483–92. <https://doi.org/10.1046/j.1365-2435.1999.00335.x>
87. Powers DR, Conley TM. Field Metabolic Rate and Food Consumption of Two Sympatric Hummingbird Species in Southeastern Arizona. *The Condor.* 1994;96:141–50. <https://doi.org/10.2307/1369071>
88. Fokidis HB, Hurley L, Rogowski C, Sweazea K, Deviche P. Effects of Captivity and Body Condition on Plasma Corticosterone, Locomotor Behavior, and Plasma Metabolites in Curve-Billed Thrashers. *Physiol Biochem Zool.* The University of Chicago Press; 2011;84:595–606. <https://doi.org/10.1086/662068>
89. Lattin CR, Pechenenko AV, Carson RE. Experimentally reducing corticosterone mitigates rapid captivity effects on behavior, but not body composition, in a wild bird. *Horm Behav.* 2017;89:121–9. <https://doi.org/10.1016/j.yhbeh.2016.12.016>
90. Rico-Guevara A, Mickley J. Bring your own camera to the trap: An inexpensive, versatile, and portable triggering system tested on wild hummingbirds. *Ecol Evol.* 2017;7:4592–8. <https://doi.org/10.1002/ece3.3040>
91. Hereward HFR, Facey RJ, Sargent AJ, Roda S, Couldwell ML, Renshaw EL, et al. Raspberry Pi nest cameras: An affordable tool for remote behavioral and conservation monitoring of bird nests. *Ecol Evol.* 2021;11:14585–97. <https://doi.org/10.1002/ece3.8127>
92. Panicker SA, Kumar RV, Ramachandran A, Padmavathi S. Analysis of Image Processing Techniques to Segment the Target Animal in Non-uniformly Illuminated and Occluded Images. In: Ranganathan G, Chen J, Rocha Á, editors. *Inven Commun Comput Technol.* Singapore: Springer; 2021. p. 15–26. https://doi.org/10.1007/978-981-15-7345-3_2
93. Bastidas-Rodriguez MX, Fernandes AM, Espejo-Urbe MJ, Abaunza D, Roncancio JS, Gutierrez-Zamora EA, et al. Estimating Wingbeat Frequency of Hummingbirds Using a No-Labeling Learning Computer Vision Approach. *Integr Comp Biol.* 2025;icaf001. <https://doi.org/10.1093/icb/icaf001>
94. Mason GJ. Species differences in responses to captivity: stress, welfare and the comparative method. *Trends Ecol Evol.* Elsevier; 2010;25:713–21. <https://doi.org/10.1016/j.tree.2010.08.011>
95. Angelier F, Parenteau C, Trouvé C, Angelier N. Does the stress response predict the ability of wild birds to adjust to short-term captivity? A study of the rock pigeon (*Columbia livia*). *R Soc Open Sci.* Royal Society; 2016;3:160840. <https://doi.org/10.1098/rsos.160840>

96. Calviño-Cancela M. Time-activity budgets and behaviour of the *Amazilia* hummingbird, *Amazilia amazilia* (Apodiformes: Trochilidae) in an urban environment. *Rev Biol Trop*. <http://creativecommons.org/licenses/by/3.0/>; 2006;54:873–8.
97. Jepsen N, Thorstad EB, Havn T, Lucas MC. The use of external electronic tags on fish: an evaluation of tag retention and tagging effects. *Anim Biotelemetry*. 2015;3:49. <https://doi.org/10.1186/s40317-015-0086-z>
98. Díaz-Salazar AF, Garzón-Agudelo F, Smiley A, Cadena CD, Rico-Guevara A. Winging it: Hummingbirds alter flying kinematics during molt. *Biol Open*. 2024;bio.060370. <https://doi.org/10.1242/bio.060370>
99. Dakin R, Segre PS, Straw AD, Altshuler DL. Morphology, muscle capacity, skill, and maneuvering ability in hummingbirds. *Science*. 2018;359:653–7. <https://doi.org/10.1126/science.aao7104>
100. Tomotani BM, Muijres FT, Johnston B, van der Jeugd HP, Naguib M. Great tits do not compensate over time for a radio-tag-induced reduction in escape-flight performance. *Ecol Evol*. 2021;11:16600–17. <https://doi.org/10.1002/ece3.8240>
101. Lamb JS, Satgé YG, Fiorello CV, Jodice PGR. Behavioral and reproductive effects of bird-borne data logger attachment on Brown Pelicans (*Pelecanus occidentalis*) on three temporal scales. *J Ornithol*. 2017;158:617–27. <https://doi.org/10.1007/s10336-016-1418-3>
102. Ropert-Coudert Y, Knott N, Chiaradia A, Kato A. How do different data logger sizes and attachment positions affect the diving behaviour of little penguins? *Deep Sea Res Part II Top Stud Oceanogr*. 2007;54:415–23. <https://doi.org/10.1016/j.dsr2.2006.11.018>
103. Weinstein BG. A computer vision for animal ecology. *J Anim Ecol*. John Wiley & Sons, Ltd; 2018;87:533–45. <https://doi.org/10.1111/1365-2656.12780>

Tables

Table 1. Black-throated Mango body masses and tag specifications, with means and standard deviations, across all trials (Behavior and Entanglement).

Item	Mean mass (grams)	Mean percent body mass
Individual before trial	7.92 ± 0.55	-
Individual after trial	8.26 ± 0.64	-
Individual across trial (averaged)	8.10 ± 0.53	-
CTT tag	0.39 ± 0.01	4.87 ± 0.30
CTT tag + harness	0.44 ± 0.02	5.49 ± 0.40
CTT tag + harness + RFID	0.48 ± 0.02	5.93 ± 0.42

Table 2. Total durations and percent of time (mean and standard deviations) that individuals spent conducting key behaviors during each treatment (tagged and untagged).

Behavior	Tagged		Untagged	
	Duration (s)	Percentage	Duration (s)	Percentage
Flying	890.34 ± 612.27	25.54 ± 17.19	1030.98 ± 748.74	29.00 ± 21.37
Perching Without Preening	2499.54 ± 634.62	71.33 ± 16.87	2485.74 ± 782.04	69.55 ± 21.75
Preening	69.33 ± 108.07	1.97 ± 3.03	17.31 ± 30.48	0.49 ± 0.86
Hover-Feeding	40.12 ± 19.42	1.15 ± 0.55	34.19 ± 20.39	0.96 ± 0.58

Table 3. Number of times that individuals conducted key behaviors (“bouts”) when tagged and untagged (mean and standard deviation for both).

Behavior	Number of Tagged Bouts	Number of Untagged Bouts
Flying	339 ± 230	362 ± 241
Perching	322 ± 231	346 ± 231
Hover-Feeding	18 ± 14	19 ± 20
Preening	22 ± 41	10 ± 16

Table 4. Length, in seconds, for each behavioral “bout” conducted by individuals when tagged and untagged (mean and standard deviation for both).

Behavior	Duration of Tagged Bouts (s)	Duration of Untagged Bouts (s)
Flying	8.44 ± 23.18	9.01 ± 30.87
Perching	284.88 ± 794.19	16.68 ± 25.92
Hover-Feeding	2.88 ± 2.52	2.34 ± 1.46
Preening	2.81 ± 4.77	1.12 ± 1.53

Table 5. Model rankings for different behavioral durations (flight, hover-feeding, and preening), with each model including the random effect of individual. Error model structures and zero-inflation terms are specified. Column headings represent: model rank (*Rank*), effects included in model (*Model*, with the following effect classifications: “Type” for treatment type, “Number” for treatment number, “Temp” for temperature within the tent, “Sucrose” for concentration of provided nectar, “Time” for period of day, “Null” for the random effect of individual, and “Global” for all variables), number of estimated parameters (*k*), log-likelihood (*LL*), Akaike’s information criterion corrected for small sample sizes (*AICc*), delta *AICc* score ($\Delta AICc$), and Akaike weight (*Weight*; indicates the level of support in favor of any given model being the most parsimonious candidate). All competitive models (within 2 $\Delta AICc$ for a given behavior) are bolded.

Rank	Model	k	LL	AICc	$\Delta AICc$	Weight
Flight (Gaussian)						
1	Number + Type	5	-380.88	773.13	0.00	0.32
2	Number + Type + Mass	6	-380.02	773.98	0.85	0.21
3	Number	4	-382.65	774.20	1.07	0.19
4	Number + Type + Mass + Sucrose	7	-378.99	774.65	1.51	0.15
5	Number * Type + Mass + Sucrose	8	-378.62	776.75	3.62	0.05
6	Type	4	-384.41	777.71	4.58	0.03
7	Null (random effect only)	3	-385.62	777.77	4.64	0.03
8	Number * Type + Mass + Sucrose + Time	10	-378.21	782.06	8.92	0.00
9	Global	11	-378.10	785.15	12.02	0.00
Feeding (Tweedie, zero-inflated)						
1	Mass	6	-200.26	414.47	0.00	0.95
2	Null (random effect only)	5	-205.36	422.08	7.62	0.02
3	Mass + Type	7	-202.99	422.65	8.18	0.02
4	Mass + Type + Temp	8	-202.30	424.10	9.64	0.01
5	Mass + Type + Temp + Sucrose	9	-201.31	425.13	10.66	0.00
6	Type	6	-205.81	425.57	11.10	0.00
7	Mass + Type + Temp + Sucrose + Number	10	-201.30	428.24	13.77	0.00
8	Mass + Type * Number + Temp + Sucrose	11	-200.76	430.46	15.99	0.00
9	Global	13	-200.33	436.78	22.31	0.00
Preening (Tweedie)						
1	Time + Type	7	-169.74	356.15	0.00	0.53
2	Time + Type + Sucrose	8	-168.96	357.44	1.29	0.28
3	Time + Type + Sucrose + Temp	9	-168.62	359.75	3.60	0.09
4	Time	6	-173.08	360.11	3.96	0.07
5	Time + Type + Sucrose + Temp + Mass	10	-168.38	362.40	6.25	0.02
6	Type	5	-176.52	364.40	8.26	0.01
7	Time + Type + Sucrose + Temp + Mass + Number	11	-168.15	365.26	9.11	0.01
8	Null (random effect only)	4	-179.83	368.54	12.40	0.00
9	Global	12	-168.15	368.74	12.59	0.00

Figures

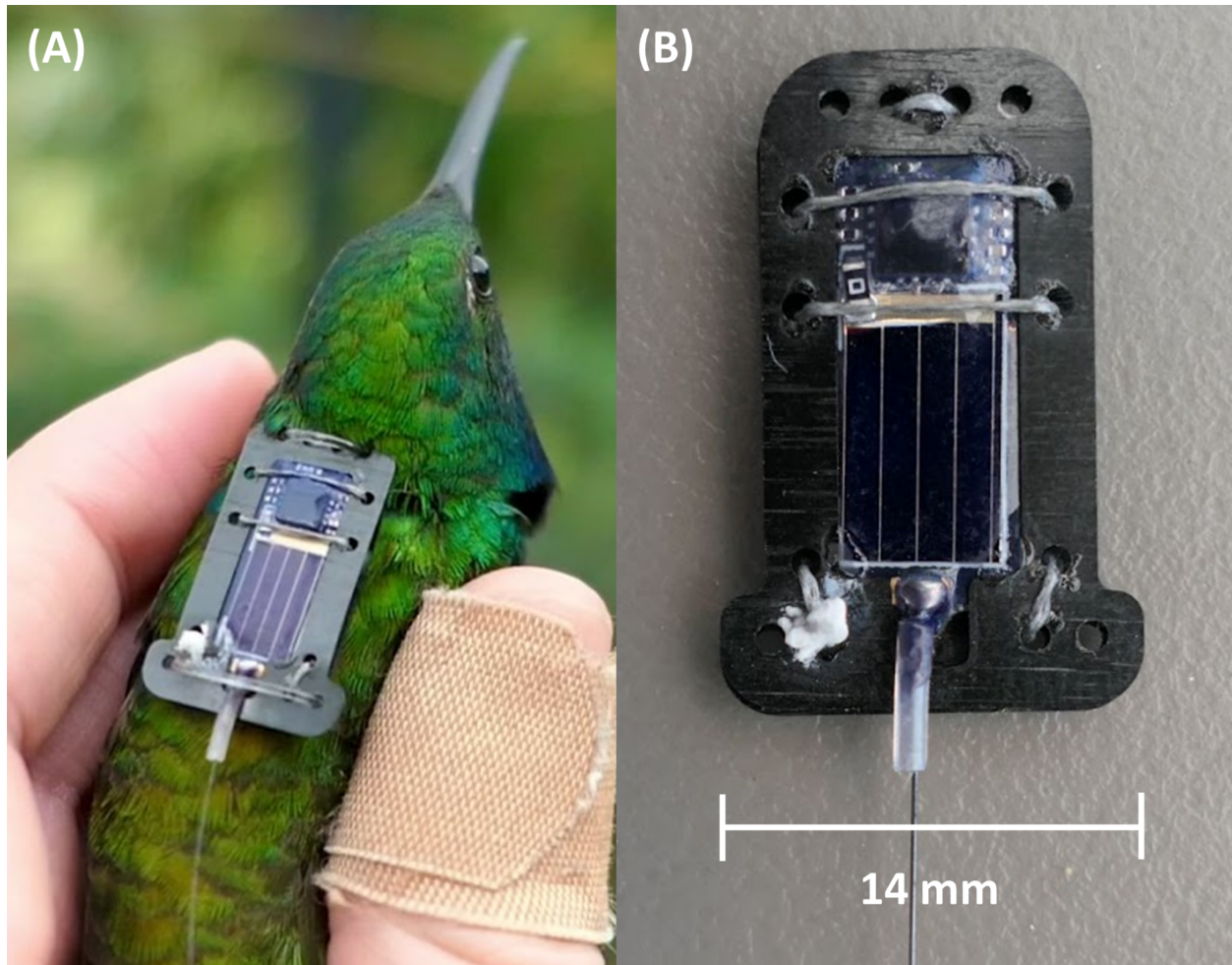


Figure 1. The radio-transmitters and birds tested in this study. (A) Adult male Black-throated Mango wearing radio-transmitter backpack with custom chassis. **(B)** Close-up view of completed chassis attachment (composed of carbon fiber reinforced polymer) on solar-powered radio-transmitter. Tag ID is cut out of the bottom chassis component; solar cell is left exposed. Four corner holes left open for the StretchMagic harness and white mark (bottom left) is dried superglue used to secure the fishing line knot.



Figure 2. Comparing Black-throated Mango behaviors when tagged and untagged. The percentage of time that individuals spent performing various behaviors is represented by pink (left-hand side for each pair) for their tagged treatment and yellow (right-hand side) for their untagged treatment. Note that “perching only” refers to perching without simultaneous preening.

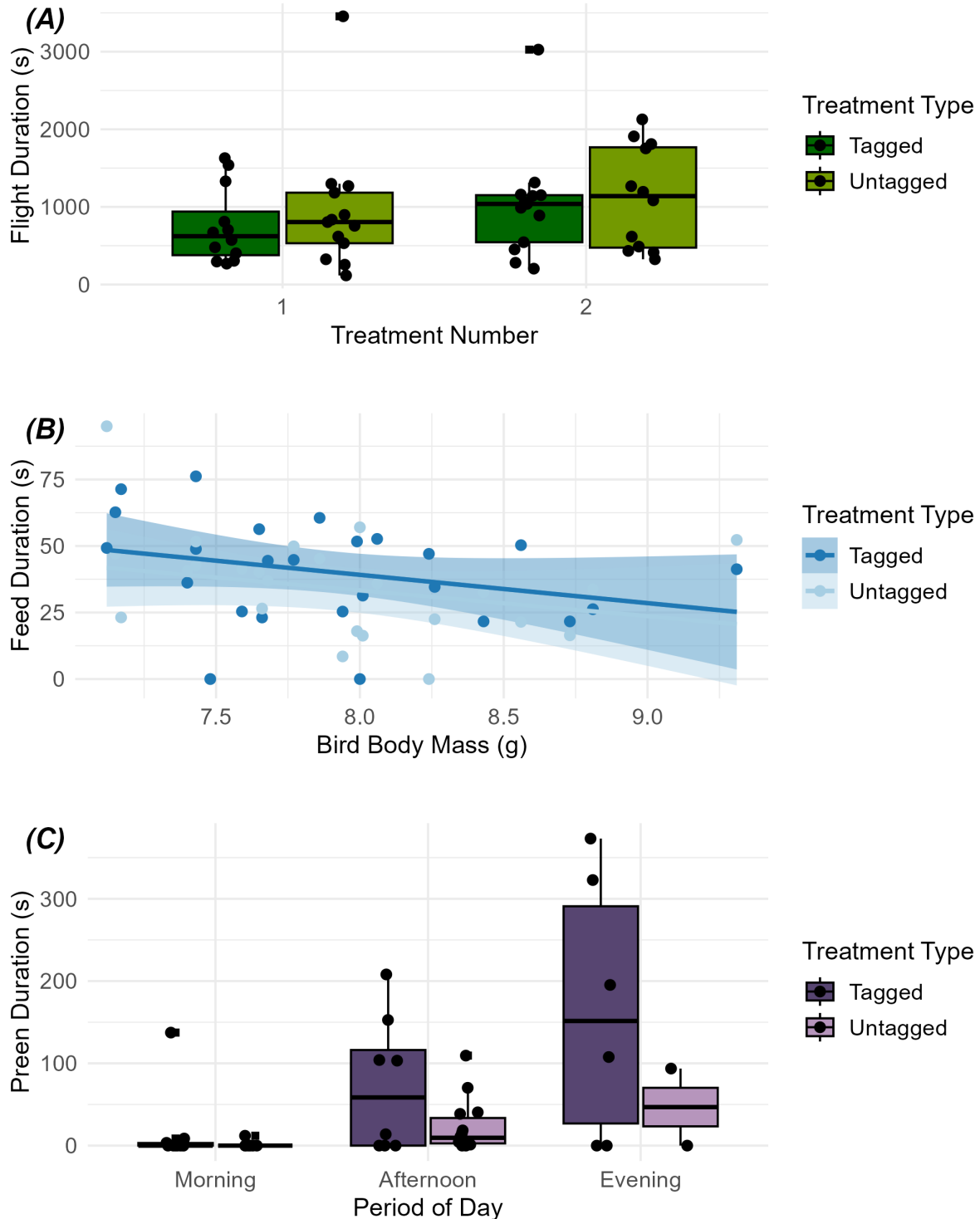


Figure 3. Hummingbird behaviors in relation to primary variables of interest. Each plot represents the best-supported model for a given behavior, assessed via AICc and likelihood ratio tests. Note that each plot's y-axis has a unique range based on the behavior in question. **(A)** Flight duration model: includes the effects of whether the bird was tagged or untagged, and whether it was undergoing its first or second treatment. **(B)** Feeding duration model: includes only the body mass of the bird. **(C)** Preening duration model: includes whether the bird was tagged or untagged, and whether the treatment occurred in the morning, afternoon, or evening.

Supplementary material

Ecuador pilot.

Study site, species, & methods.

In the dry season of August and September 2022, we conducted an observational pilot study of radio-transmitter backpack harness ethics at Un poco del Chocó Estación Biológica (UPDC). At roughly 1,200 m elevation in a transition zone between the Chocó and Tropical Andes hotspots, UPDC is situated alongside the Pachijal River in moderately disturbed, primary lower montane rainforest. We chose to study the Green-crowned Brilliant (*Heliodoxa jacula*), White-necked Jacobin (*Florisuga mellivora*), and White-tipped Sicklebill (*Eutoxeres aquila*) on account of their large body sizes and their varied systematics (each species occupies one of the nine major clades of hummingbirds: Brilliants, Topazes, and Hermits, respectively [1]). In this case, we did not selectively capture adults or males (see **Table S1**). While we sexed individuals based on plumage characteristics, we note that there are recorded cases of male-plumaged females in White-necked Jacobins [2], and that White-tipped Sicklebills are sexually monomorphic [3].

For this experiment, we captured, measured, and radio-transmitter harnessed all hummingbirds as outlined in the main text, but here we identified individuals based on bands as opposed to passive integrated transponders. Our experimental setup was a similar, reduced version of that described in the main text: we constructed our flight arena (Coleman tent) inside the research center, containing a hummingbird feeder (provided sucrose solution measured with a refractometer at the beginning of each trial) and a perch. At the start and end of each trial, we recorded the temperature at the peak of the tent interior using a handheld thermometer. We next released the tagged individual into the flight tent, then manually observed and logged the presence of our behaviors of interest (flying, perching, feeding, and preening) over the trial duration as follows: continuously for hours 0–2 and, if applicable, 5-minute checks once every 15 minutes for hours 2–4, 5-minute checks once every 30 minutes for hours 4–6, and then 10-minute checks once every 60 minutes for the remainder of the trial (see **Table S1**). In the case of overnight trials, however, we left birds undisturbed until early morning after determining that they had fallen asleep (using a red light to minimize any disturbance).

Note that, as we used a hummingbird feeder as opposed to a syringe, birds perched rather than hovered while feeding. Additionally, given that sicklebills are not known to visit feeders, and the ones in our trial were no exception, we fed each individual by hand once every 30 minutes—an interval that we selected to balance sufficient energetic intake against the stress of recapture inside the tent.

Results & significance.

In total, we captured, tagged, and monitored 6 Green-crowned Brilliants (1 adult female, 4 adult males, 1 juvenile of unknown sex), 4 White-necked Jacobins (4 adult males), and 3 White-tipped Sicklebills (all juveniles of unknown sex). Given that this study was observational and our methods differed substantially from those implemented in Colombia, we have elected to reserve our basic results to the supplementary materials here (**Table S1**), and we include them primarily to showcase that there were no drastic behavioral deviations from that which we observed with Black-throated Mangoes, despite the birds' systematic differences.

Average trial lengths, in hours, were as follows: 11.50 ± 10.91 for brilliants, 1.56 ± 0.89 for jacobins, and 4.00 ± 2.00 for sicklebills. While brilliants lost an average of 0.06 ± 0.20 grams across their trials, jacobins and sicklebills gained an average of 0.17 ± 0.15 and 0.74 ± 0.67 grams, respectively. Out of these 13 total individuals, 3 brilliants and 1 jacobin did not preen at all. This result is not inconsistent with what we found

in Colombia: 12 of our 25 mangoes exhibited no preening during their tagged observation period (although it is possible that they preened during their 30-minute acclimation period, which we did not film). Beyond this behavior, all individuals exhibited flying, perching, and autonomous feeding (except one, see below), or, in the case of sicklebills, were hand-fed. None of our birds, including those undergoing overnight trials, displayed any of the signs of distress characterized by Russell et al. [4].

As described in the main text, we did observe one instance of harness issues, when a White-necked Jacobin's attempts to preen beneath the harness (sized according to the suggestions of Williamson and Witt [5]) resulted in its bill becoming stuck under the StretchMagic. Indeed, after immediately removing the harness and replacing it with a snuggler one, the jacobin began preening again and became stuck once more moments later. We removed this second harness and released the bird promptly, resulting in a curtailed, 0.22-hour trial wherein the bird did not feed at all. Based on these events, we suspect that, owing to birds' many cervical vertebrae [6] and subsequent capacity for head flexion [7], there is an inherent risk to utilizing three-loop harnesses with such proportionally long-billed birds.

Although there have been some studies of Green-crowned Brilliant and White-necked Jacobin behavior, they are largely focused on aggression and dominance [2,8,9]. Research on White-tipped Sicklebills, meanwhile, has been more limited to sighting and feeding records [10–12], given the elusive nature of the sicklebill species [7,13]. While our results do not provide in-depth insight into the daily behaviors of these species either, they are a first step towards understanding how diverse hummingbirds may respond to biologging devices. We strongly believe that comprehensive studies of species-specific effects in relation to biologgers are not only warranted, but critical.

Harness and device chassis design.

Assemblage.

Adapting from Williamson and Witt [5], we designed our harness to operate with a device that **a)** is solar-powered and can withstand multi-year deployments in the field, and **b)** does not come with prefabricated loops—and thus, any long-term means of attachment to an individual bird. As such, we opted for a top and bottom custom chassis (structural framework) that we could thread around our radio-transmitter (Cellular Tracking Technologies “LifeTag”), effectively pinning it in place while keeping the solar cell fully exposed. We designed our chassis to ensure minimal chafing and drag [14], emphasizing a thin, streamlined nature, rounded corners, and open spaces where possible, to reduce weight without compromising durability.

We designed each chassis (14 mm wide, 22 mm long) individually in Autodesk AutoCAD, a 2D drafting software with DXF file support (other free and open-source options include QCAD and Inkscape), to include **1)** 1-mm diameter holes for the harness and thread, and **2)** each tag's unique identification number (**Fig. S4**). Using a diode-pumped, solid-state, pulsatile laser operating at a wavelength of 355 nm, with a spot size (minimum cut width) of 10 μm , we laser cut each chassis from carbon fiber reinforced polymer (CFRP), which was fabricated with a layup of “prepreg” (fibers pre-impregnated with a thermosetting resin matrix) 27 gsm carbon fiber sheets. We stacked 3 sheets and cured them at 80 psi/150 $^{\circ}\text{C}$, in 0-90-0 configuration to make the chassis stronger in one direction than the other (more rigid along the length, 0 $^{\circ}$; more flexible along the width, 90 $^{\circ}$). The resulting cured sheet is $\sim 90\ \mu\text{m}$ in thickness. It is worth noting that LifeTags are manufactured with a thin coating of epoxy for waterproofing purposes, which acts as an insulating barrier between the conductive CFRP chassis and the tags' circuit components.

We recommend conducting assembly in a setting with access to tools such as a fine-precision scale ($\sim 10\ \text{mg}$ accuracy), which we used to weigh the tag throughout the construction process. For thread, we chose ultrathin, braided fishing line (KastPro), with a minute application of cyanoacrylate superglue at the tip to

avoid fraying. Leaving the four corner holes open for the harness material (0.7 mm StretchMagic), we looped the fishing line through the chassis holes dotted around the LifeTag's perimeter, particularly across its width and in diagonals across the sides, to ensure tight contact between each chassis layer and the tag (**Fig. 1** main text). Throughout this process, we used blunt-end (to avoid fraying), electrostatic-discharge-safe tweezers to guide the fishing line. We opted to add glue via a wire applicator to any knots tied with the fishing line, major points where the thread interacted with the tag, and any places where the tag interacted heavily with the chassis. Notably, we previously used marine epoxy (UV- and water-resistant) but have since discovered that it is heavy, short-lived, and peels easily.

All told, the addition of the chassis, thread, and glue added a total of ~53 mg to each tag (**Table 1** main text).

Significance, limitations, and future research.

With the increasing accessibility of miniature animal tracking devices, researchers must continue to refine safe, ultralight attachment methods [5]. When fabricating micromaterials for wildlife applications, there is a continuous tradeoff between weight, durability, and ergonomics (e.g., an overly thin harness thread could cut into a bird's skin, while a slim and narrow chassis, prone to breakage, could impose fewer deleterious device effects). When working with small-bodied birds or insects, there are often few alternatives to glue-on attachment methods, which have unpredictable longevity—although there are countermeasures to increase retention, such as plucking feathers for direct contact with the bird's skin, and gluing or sewing the tag to a gauze or fabric base to increase the connected surface area [15]. In this way, glue-based attachment may be sufficient for miniature radio-transmitters with rapid beep rates and correspondingly short lifespans (< 2–3 months; Lotek, Cellular Tracking Technologies).

In solar-powered tags, however, multi-year deployments are entirely possible (as they are for GPS tags, e.g., [5]), and a flexible, alternative design is essential. As the addition of loops/tubes for harness threading can be too complicated for the manufacturing process or can make tags prohibitively heavy, our chassis design minimizes weight while maximizing longevity and UV capture. CFRPs have a high strength-to-weight ratio—which allows for a very strong yet lightweight chassis—and have a high corrosion resistance, making the chassis resilient to the elements. The combination of cyanoacrylate glue and thread also ensures a longer lifespan, as the former is brittle once cured and does not hold well to bending stresses, while the latter could unravel without additional securement. This ultra-lightweight chassis design, which is easily customizable depending on research needs and tag size/shape, allows us to study a greater expanse of small, previously untestable animals.

Given the rapid technological advancement in the world of biologging [16], we are confident that tags and their associated attachment methods (such as our chassis) can continue to be further improved and streamlined, not only in weight, but also in footprint. Researchers biologging ever-smaller volant animals must ensure that the full range of wing amplitude (e.g., see [17] for hummingbird-specific figures) is in no way obstructed by their devices. Indeed, since conducting this study in 2022, commercially available tags have already been greatly miniaturized, making the tagging process for animals—flighted or not—much safer and more straightforward. As an additional note, although Williamson and Witt [5] found no evidence of deleterious effects for hummingbirds wearing backpack harnesses after 1–2 years, we advise minimizing deployments and maximizing recapture efforts at the termination of each study, owing to the ethical trade-off of individuals wearing tags for multiple years, or even a lifetime.

Future studies may also benefit from an updated harness design, particularly for short-, straight-billed species. In Ecuador, we observed a White-necked Jacobin's bill become wedged under the neck-loop while preening (see **Table S1**), impairing the bird's subsequent attempts at flight. With exposed culmens measuring 16.63 ± 0.80 mm in length, our White-necked Jacobins had shorter/straighter bills than their

experimental counterparts (Black-throated Mangoes: 22.44 ± 1.01 mm, Green-crowned Brilliants: 24.03 ± 1.17 mm; the extreme curvature of White-tipped Sicklebills' beaks prevented them from becoming stuck). A backpack harness that conjoins over the sternum rather than incorporating a neck-loop—similar to those used with many raptors [18,19]—may be more suitable; however, a thorough ethical study of this approach is warranted.

Regardless of the design, any space between the bird's body and the harness itself—with or without the neck-loop—may lead to entanglement issues, even if it is as small as a few millimeters (as per the recommendations of Williamson and Witt [5]). Our personal observations indicate that hummingbirds are least aware of their surroundings and most likely to come into contact with other objects while in combat with rival individuals. Given that hummingbirds—particularly territorial individuals, like in most of our focal species [8,20,21]—rely on extreme maneuverability, agility, and energy-use for frequent aggressive encounters [22,23], we propose that a valuable follow-up entanglement test would also involve dyadic “competition trials” that spur agonistic behavior, like those designed by Gaffney [24].

Supplementary references.

1. McGuire JA, Witt CC, Remsen JV, Corl A, Rabosky DL, Altshuler DL, et al. Molecular Phylogenetics and the Diversification of Hummingbirds. *Curr Biol*. 2014;24:910–6.
2. Falk JJ, Webster MS, Rubenstein DR. Male-like ornamentation in female hummingbirds results from social harassment rather than sexual selection. *Curr Biol*. 2021;31:4381-4387.e6.
3. Betancourth-Cundar M, Beltran-Arevalo B-A, Torres-Sánchez P. White-tipped Sicklebill (*Eutoxeres aquila*). *Birds World* [Internet]. 2020 [cited 2021 Feb 16]; Available from: <https://birdsoftheworld.org/bow/species/whtsic1/cur/introduction>
4. Russell SM, Russell RO, Pollock J, Hill A. The North American Banders' Manual for Hummingbirds [Internet]. Point Reyes Station, California, USA; 2019. Available from: [efaidnbmnnnibpcajpcglclefindmkaj/https://www.nabanding.net/wp-content/uploads/2019/11/Hummingbird-Manual-31_Oct_2019.pdf](https://www.nabanding.net/wp-content/uploads/2019/11/Hummingbird-Manual-31_Oct_2019.pdf)
5. Williamson JL, Witt CC. A lightweight backpack harness for tracking hummingbirds. *J Avian Biol* [Internet]. 2021 [cited 2022 Oct 31];52. Available from: <https://onlinelibrary.wiley.com/doi/abs/10.1111/jav.02802>
6. Marek RD, Falkingham PL, Benson RBJ, Gardiner JD, Maddox TW, Bates KT. Evolutionary versatility of the avian neck. *Proc R Soc B Biol Sci*. 2021;288:20203150.
7. Boehm MMA, Guevara-Apaza D, Jankowski JE, Cronk QCB. Floral phenology of an Andean bellflower and pollination by buff-tailed sicklebill hummingbird. *Ecol Evol*. 2022;12:e8988.
8. Falk JJ, Rubenstein DR, Rico-Guevara A, Webster MS. Intersexual social dominance mimicry drives female hummingbird polymorphism. *Proc R Soc B Biol Sci*. 2022;289:20220332.
9. Fernandez-Duque F, Miller ET, Fernandez-Duque M, Falk J, Venable G, Rabinowicz S, et al. Phenotype predicts interspecific dominance hierarchies in a cloud-forest hummingbird guild. *Ethology*. 2024;130:e13410.
10. Stiles FG. Ecology, Flowering Phenology, and Hummingbird Pollination of Some Costa Rican *Heliconia* Species. *Ecology*. 1975;56:285–301.
11. Vigle GO. A Nest of *Eutoxeres aquila heterura* in Western Ecuador. *The Auk*. 1982;99:172–3.
12. Rengifo C, Bakermans MH, Puente R, Vitz A, Rodewald AD, Zambrano M. First Record of the White-tipped Sicklebill (*Eutoxeres aquila aquila*: Trochilidae) for Venezuela. *Wilson J Ornithol*. 2007;119:292–5.
13. Stiles FG. The Annual Cycle in a Tropical Wet Forest Hummingbird Community. *Ibis*. 1980;122:322–43.
14. Vandenabeele SP, Shepard ELC, Grémillet D, Butler PJ, Martin GR, Wilson RP. Are bio-telemetric devices a drag? Effects of external tags on the diving behaviour of great cormorants. *Mar Ecol Prog Ser*. 2015;519:239–49.
15. Hadley AS, Betts MG. Tropical deforestation alters hummingbird movement patterns. *Biol Lett*. 2009;5:207–10.
16. Kays R, Crofoot MC, Jetz W, Wikelski M. Terrestrial animal tracking as an eye on life and planet. *Science*. 2015;348:aaa2478.
17. Díaz-Salazar AF, Garzón-Agudelo F, Smiley A, Cadena CD, Rico-Guevara A. Winging it: Hummingbirds alter flying kinematics during molt. *Biol Open*. 2024;bio.060370.
18. Humphrey JS, Avery ML. Improved Satellite Transmitter Harness Attachment Technique. *J Raptor Res*. 2014;48:289–91.
19. Stewart MT, Millsap BA. Challenges Adapting a Backpack Harness for Use on Gray Hawks (*Buteo plagiatus*). *J Raptor Res*. 2021;56:111–5.
20. Greeney HF, Schuchmann K-L, Kirwan GM. Black-throated Mango (*Anthracothonax nigricollis*), version 1.1. *Birds World* [Internet]. 2022 [cited 2022 Nov 2]; Available from: <https://birdsoftheworld.org/bow/species/bltman1/cur/introduction>
21. Taylor J. Green-crowned Brilliant (*Heliodoxa jacula*). *Birds World* [Internet]. 2020 [cited 2021 Feb 17]; Available from: <https://birdsoftheworld.org/bow/species/grcbri1/cur/introduction>

22. Segre PS, Dakin R, Zordan VB, Dickinson MH, Straw AD, Altshuler DL. Burst muscle performance predicts the speed, acceleration, and turning performance of Anna's hummingbirds. Fernald R, editor. *eLife*. 2015;4:e11159.
23. Sargent AJ, Groom DJE, Rico-Guevara A. Locomotion and Energetics of Divergent Foraging Strategies in Hummingbirds: A Review. *Integr Comp Biol*. 2021;61:736–48.
24. Gaffney A. The effects of atmospheric pressure on inter-specific competition and the morphological and hematological characteristics of elevational distributions of hummingbirds. *Biol ETDs* [Internet]. 2017; Available from: https://digitalrepository.unm.edu/biol_etds/198

Supplementary tables.

Table S1. Overview of Ecuadorian pilot study. Column headings represent: species names in Latin (*Species*); bird's sex classification of F. for female, M. for Male, or U. for unknown (*Sex*); bird's age classification of Ad. for adult or Juv. for juvenile (*Age*); trial replicate for a given species (*Trial*); total time in hours that each bird was tested wearing the backpack harness, with * indicating that the trial included overnight testing (*Trial length [h]*); trial's temporal classification of Morn. for morning, Aft. for afternoon, or Eve. for evening, or some combination thereof (*Period of day*); temperature in Celsius within the tent, averaged across beginning and end of each trial (*Temp. [°C]*); w/w sugar-water content of provided nectar (% sucrose); behaviors present throughout trial, checked with X to indicate presence, - to indicate absence, or Handfed to indicate the individual was fed by hand (*Behaviors Exhibited: Flying, Perching, Feeding, Preening*); any point that an individual's bill became caught in the neck-loop of the harness (*Harness Issues*), and the amount of weight in grams that the bird gained/lost throughout the trial (*Weight change [g]*).

Species	Sex	Age	Trial	Trial length (h)	Period of day	Temp. (°C)	% sucrose	Behaviors Exhibited				Harness issues	Weight change (g)
								Flying	Perching	Feeding	Preening		
<i>H. jacula</i>	F.	Ad.	1	2	Aft.	26.2	22	X	X	X	-	-	+ 0.31
	M.	Ad.	2	2	Aft.	23.6	22	X	X	X	-	-	- 0.09
	M.	Ad.	3	2	Morn.	25.0	22	X	X	X	-	-	- 0.09
	M.	Ad.	4	15*	Eve – Morn.	18.6	22	X	X	X	X	-	- 0.27
	U.	Juv.	5	24*	All	18.3	22	X	X	X	X	-	- 0.18
	M.	Ad.	6	24*	All	19.8	22	X	X	X	X	-	- 0.01
<i>F. mellivora</i>	M.	Ad.	1	2	Morn.	27.6	21	X	X	X	X	-	+ 0.06
	M.	Ad.	2	2	Eve.	21.2	21	X	X	X	-	-	+ 0.32
	M.	Ad.	3	2	Morn.	18.8	22	X	X	X	X	-	+ 0.29
	M.	Ad.	4	0.22	Aft.	23.8	22	X	X	-	X	X	- 0.02
<i>E. aquila</i>	U.	Juv.	1	2	Aft.	24.0	21	X	X	Handfed	X	-	- 0.09
	U.	Juv.	2	4	Aft.	22.0	21	X	X	Handfed	X	-	+ 1.43
	U.	Juv.	3	6	Morn. – Aft.	21.6	23	X	X	Handfed	X	-	+ 0.71

Table S2. Parameter estimates, standard errors (SE), 95% confidence intervals (CI), and Benjamini-Hochberg-corrected p-values (p) for the top-ranked models described in the main text for flight, hover-feeding, and preening durations, as determined using Akaike's information criterion adjusted for small sample sizes (AICc). All parameters with significant effect sizes (95% confidence intervals not overlapping zero and, subsidiarily, a p-value < 0.05) are bolded.

Parameter	Estimate	SE	Lower 95% CI	Upper 95% CI	p
Flight ~ Treatment Number + Treatment Type (Gaussian)					
β Intercept	776.60	138.10	498.01	1055.19	7.83e-06
β Untagged	149.39	76.61	-6.72	305.49	0.0703
β Treatment 2	218.74	76.61	62.64	374.84	0.0111
Feeding ~ Bird Weight (Tweedie, zero-inflated)					
β Intercept	5.98	0.88	4.27	7.70	3.71e-11
β Weight	-0.29	0.11	-0.51	-0.07	0.0111
Preening ~ Time of Day + Treatment Type (Tweedie)					
β Intercept	4.41	0.41	3.59	5.23	1.80e-15
β Untagged	-1.37	0.50	-2.36	-0.39	0.0111
β Morning	-1.98	0.60	-3.17	-0.80	0.0023
β Evening	0.72	0.55	-0.36	1.81	0.1916

Supplementary figures.

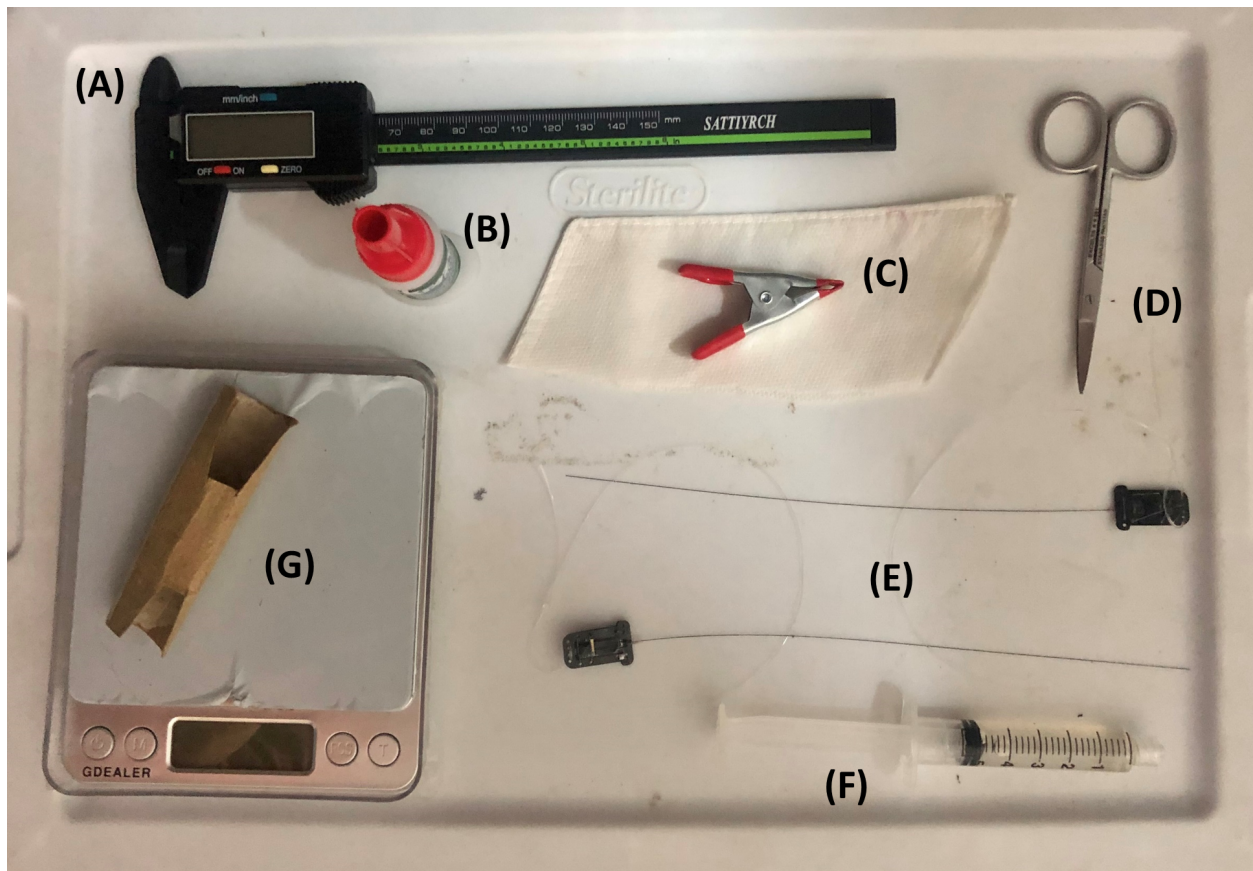


Figure S1. Materials used for harness application process. From top-left clockwise: **(A)** calipers to measure harness, **(B)** superglue to secure knots, **(C)** cloth strip and clamp to swaddle bird while tying final harness knot, **(D)** scissors to trim StretchMagic harness once tied, **(E)** LifeTags with prefabricated neck-loops of two sizes to customize for each individual bird, **(F)** prepared syringe with sugar water for if the individual showed any sign of stress (e.g., blinking slowly), and **(G)** scale with cardboard tube to weigh each individual (cutouts were to accommodate the tag on the back post-harnessing).



Figure S2. Load cell setup in enclosed-environment tent. We coated the syringe on the left-hand side with red tape and added yellow tape to its tip to mimic floral appearances, thereby drawing the hummingbird's attention more readily. We deliberately spaced the perch (right-hand side) far enough from the feeder such that the bird could not perch and feed simultaneously.



Figure S3. Aviary-style enclosure (3.3 x 2.7 x 2.0 m) used for entanglement and overnight harness tests. Feeders and local vegetation are included inside.

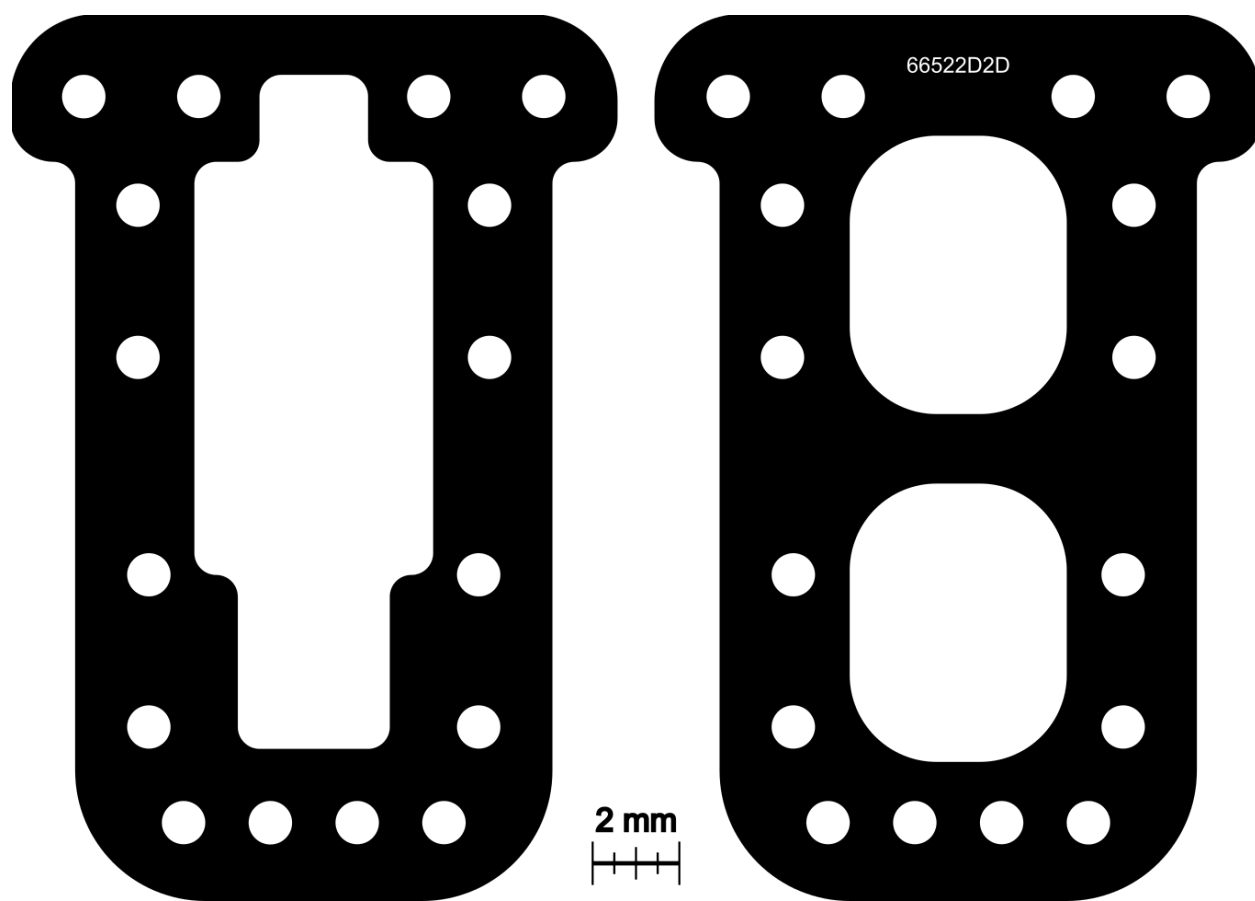
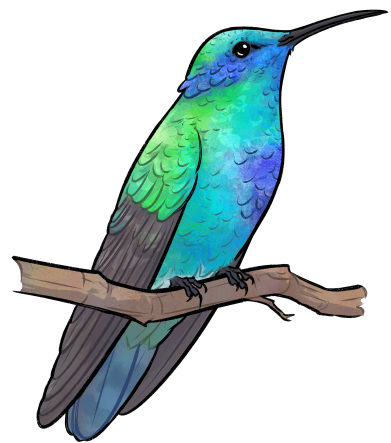
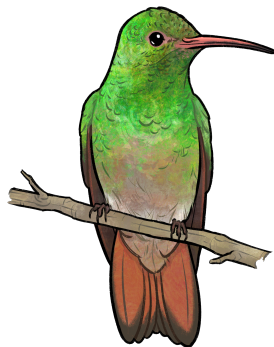
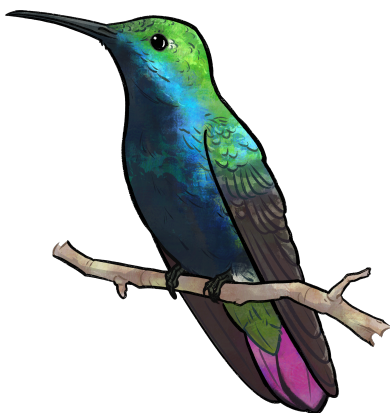
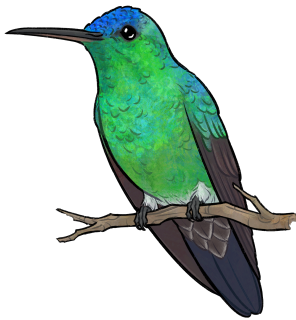
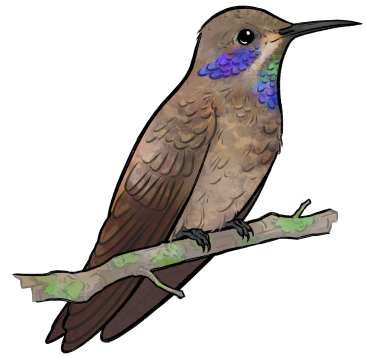
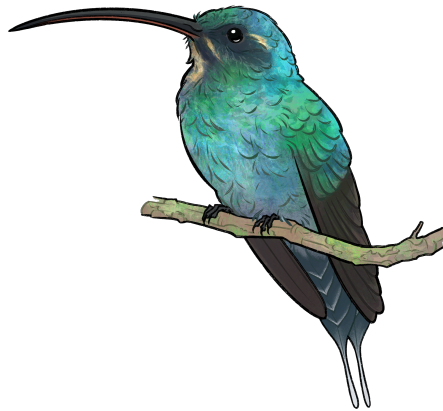
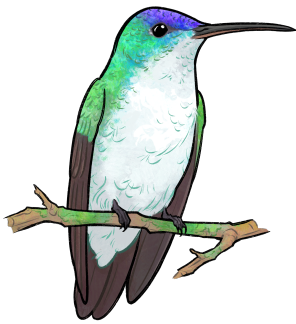
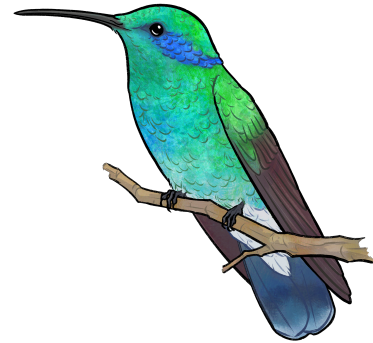


Figure S4. Example AutoCAD mock-up for top and bottom chassis of a specific radio-transmitter.

Supplementary video.

Video S1. Sample behaviors delineated in BORIS video processing. Video clips include flying, hover-feeding, preening, and perching (2 bouts). Video can be found in official *Animal Biotelemetry* publication [here](#).



Chapter III: The unequal cost of scarcity: how individual hummingbirds across an assemblage respond to experimental feeder removal

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References formatted as per *Behavioral Ecology* standards.

Abstract

Background: Hummingbirds, renowned for their aggression and resource monopolization, provide a useful case study for questions regarding highly competitive systems. We designed a 21-day experiment to examine how their visitation patterns might shift within and across species when confronted with variable artificial resource availability and an associated competitive bottleneck.

Methods: Operating within a thriving hummingbird assemblage in the Colombian Andes, we progressively removed and reinstated feeders equipped with radio-frequency identification (RFID) antennas in a mirrored fashion (7 three-day periods: 16 → 12 → 8 → 4 → 8 → 12 → 16 feeders). Throughout these three weeks, we tracked the visits of 109 RFID-tagged individuals that spanned six species. We analyzed their behavioral responses via eight *a priori* questions that encompassed individual, species, and assemblage levels, focusing on components such as how a bird's feeder access at the start of the experiment changed under scarcity and elevated competition, whether birds with little baseline access were more likely to cease visiting for at least one day ("drop out"), if birds partitioned diurnal hours to better access the resources, whether visitation strategies formed a spectrum and what it consisted of if so, and if a species' niche breadth along multiple axes would make it more or less vulnerable to scarcity.

Results: Daily feeder visits rose roughly 2.3x under scarcity. Across the experiment, birds with greater initial access were estimated to maintain ~4.7x more time at the feeders and be ~800x less likely to drop than low-access birds. Rather than temporally partition to increase feeder access, birds compressed their activity windows under scarcity—especially low-access birds, which started up to 278 minutes later and ended up to 167 minutes earlier than high-access ones—while species with shorter activity windows (narrower niche breadths) were far more likely to drop out at some point. Visitation strategies did indeed form a continuum of repeatable individual signatures, even as the assemblage shifted towards greater feeder fidelity, fewer and less revisitation-heavy visits, and shorter bouts when there were fewer options. Many of these aspects of behavior did not fully recover as we reinstated feeders—likely due, in part, to 35 of the original 109 individuals remaining undetected once the experiment had ended.

Conclusions: The costs of scarcity fell most heavily on low-access individuals and certain species, with experimental carryover prevalent in many of our metrics by the end of the 21 days. Our results suggest that hummingbird assemblages accustomed to using feeders might buffer against sudden resource loss through hierarchical filtering, which raises questions of whether certain subsets of the Trochilidae are similarly vulnerable in natural floral systems, which currently face many anthropogenic threats and are in constant flux.

Introduction

Competition is a central force that shapes the life of every organism (Keddy 2001), with animals only able to stably coexist if they differ in their abilities to consume or control access to limited resources (Titman 1976; Tilman 1987). Asymmetric competition, in particular, arises when one party is dominant over the other (Keddy 2001); under sufficient stress, these competitive asymmetries can translate to “hierarchical filtering,” wherein the superior competitors of a population or assemblage are more equipped to withstand the adverse conditions, while the inferior ones are squeezed out of the system entirely (Milles et al. 2023). In light of the Anthropocene (Lewis and Maslin 2015), replete with rapid, human-driven land use (Foley et al. 2005) and climate change (Walther et al. 2002; Parmesan and Yohe 2003), that pressure is now ubiquitous, unnaturally inflating competition over a shrinking pool of resources (Valeix 2011; Ferry et al. 2016; Gilbert et al. 2022; Delgado-Martínez et al. 2023). It is essential that we ramp up our efforts to understand how individuals and species will behaviorally cope when faced with instability or scarcity (Twinomugisha et al. 2006), and which will become “winners” and “losers” in the process (Di Cecco and Hurlbert 2022).

Hummingbirds offer a compelling case study for investigations of asymmetric competitive abilities under variable resource availability, for reasons that are inherently intertwined. First and foremost, these tiny birds are under extreme energetic pressure: with the highest mass-specific metabolic demands across vertebrates (Suarez et al. 1990; Suarez et al. 1991; Suarez 1992), a single hummingbird can consume as many as 187 small meals and up to 1.6–5.4x its own bodyweight in fluid just to get through one day (Beuchat et al. 1979; Krebs and Harvey 1986; Powers and Nagy 1988; Weathers and Stiles 1989; Beuchat et al. 1990; Powers and Conley 1994; McWhorter and Martínez del Rio 1999). A hummingbird must therefore have frequent and prodigious access to nectar to survive (Elting et al. 2026). In times of abundance, hummingbird assemblages can be large (Abrahamczyk and Kessler 2010; Remolina-Figueroa et al. 2022), crowded (Stiles and Wolf 1970; Lara et al. 2011; Lanna et al. 2017), and shaped by fiercely competitive dominance hierarchies (Rodríguez-Flores and Arizmendi Arriaga 2016; Bribiesca et al. 2019; Márquez-Luna et al. 2019; Tellez-Colmenares et al. 2025 preprint), wherein certain species can more consistently exclude others from resources by virtue of agonistic behaviors and superior competitive ability (Smith and Parker 1976; Pimm et al. 1985; Tellez-Colmenares et al. 2025 preprint). Yet in times of scarcity, these assemblages shrink—with many species emigrating or being otherwise excluded from the system (Abrahamczyk and Kessler 2010; Abrahamczyk and Kessler 2015)—and the subset that remains must quickly adapt to the new energetic landscape (Justino et al. 2012).

How these dynamics play out on an individual scale, however, has been comparatively understudied. Even within a single species, hummingbirds can vary substantially in their dominance capabilities (Tellez-Colmenares et al. 2025 preprint) and foraging strategies (Gowda et al. 2012; Betts et al. 2015; Falk et al. 2025 preprint); indeed, individuals themselves display remarkable behavioral plasticity and are capable of shifting between multiple feeder-visitation or movement strategies quite rapidly (Falk et al. 2025 preprint; Rueda-Urbe et al. 2026). While this individual flexibility undoubtedly extends to conditions of resource loss and the increased competition that accompanies them (Ewald and Carpenter 1978; Garrison and Gass 1999; Justino et al. 2012; Sargent et al. 2021), only a handful of studies have actually tracked unique hummingbird responses to a perturbation (Hadley and Betts 2009; Volpe et al. 2014; Hazlehurst and Karubian 2018)—and fewer still have done so across an assemblage. This is due in large part to

the fact that biologgers have only recently miniaturized enough to track these tiny birds (Sargent et al. 2026), as well as the reality that manual or automated radio-telemetry experiments on such a scale would be both costly and logistically challenging (Sargent et al. 2021); as such, what the individual hummingbird experience might look like during scarcity, and which specific birds might get filtered out of the system, are largely unknown.

Radio-frequency identification (RFID) technology—which uses electromagnetic fields to detect uniquely coded RFID tags at sub-second levels—serves as an alternative, more cost-effective means of addressing this gap (Harrison and Kelly 2022). Hummingbirds are prone to visiting and relying on artificial sugar-water feeders (Sonne et al. 2016), which offer tractable means of conducting ecologically relevant experiments on free-living hummingbirds (e.g., Pimm 1978; Maglianesi, Böhning-Gaese, et al. 2015; Weinstein and Graham 2016); with each feeder equipped with an RFID antenna, we can automatically log the feeding visits of individuals that have been permanently implanted with an ultraminiature RFID tag (often referred to as a passive integrated transponder). This technology thus operates at extremely precise spatiotemporal resolutions and allows us to capture which birds visit which feeders, at what times, and for how long, and thereby examine the idiosyncratic foraging patterns of many individuals simultaneously (Rousseu et al. 2014; Bandivadekar et al. 2018; English et al. 2022; Falk et al. 2025 preprint). Here, we designed a field experiment to determine how individual hummingbirds, representing a multi-species assemblage in the Colombian Andes, would respond as we progressively removed and reinstated feeders from an array of 16 units. We organized our analysis around eight *a priori* questions that spanned individual, species, and assemblage levels, as detailed in Box 1 below.

Box 1. Our eight behavioral questions and their corresponding predictions.

Competition and access under scarcity

Q1. Will competition measurably rise at feeders when there are fewer available? Will feeders have more visitors and visits during scarcity?

Prediction: *Yes to both: reduced resource availability concentrates competition at the remaining options* (Boag and Grant 1984; Valeix 2011; Ferry et al. 2016; Delgado-Martínez et al. 2023).

Q2. Will “high-access” individuals from period A maintain proportionally higher access throughout the experiment, even during scarcity? Within species, will access correlate with body mass?

Prediction: *Yes: high-access birds will maintain higher access, like in persistent dominance hierarchies* (Rodríguez-Flores and Arizmendi Arriaga 2016; Márquez-Luna et al. 2019); *within species, larger birds will hold more access given their physical advantage* (Bribiesca et al. 2019).

Q3. Will “low-access” individuals from period A be

Temporal niche

Q5. Will individuals establish temporal partitioning, influenced by access? Will low-access birds rise earlier or stay later (especially during scarcity)? Will this represent active partitioning, or clustering at dawn/dusk driven by circadian rhythms?

Prediction: *Low-access birds will rise earlier and stay later, representing active temporal partitioning rather than passive circadian-driven clustering: subordinate competitors can shift to marginal foraging windows when in the presence of dominants* (Lara et al. 2009; Maziarz et al. 2023).

Foraging strategy

Q6. Will individuals adjust their foraging strategies across the experiment? Will strategies be stable across periods, or will they shift? Which components will be repeatable individual traits?

Prediction: *Individuals will adjust foraging strategies—which will form a continuum—under scarcity, with flexibility across conditions* (Sargent

excluded from the system as feeders dwindle?

Prediction: Yes: low-access birds will drop out under scarcity, given that interference competition can lead to lower-ranking individuals being excluded (Pimm et al. 1985; Carpenter et al. 1993; Camfield 2006), especially when resources dwindle (Powers and McKee 1994).

Preference reestablishment

Q4. Will individuals reestablish preference for particular feeders as they are reinstated, or will new individuals establish greater access to the returned feeders?

Prediction: Original individuals will reclaim their preferred feeders, given that hummingbirds maintain strong fidelity to specific nectar sources within their foraging ranges (Garrison and Gass 1999; Gowda et al. 2012; Bandivadekar et al. 2018).

et al. 2021). Some behavioral traits will be more repeatable than others (Bell et al. 2009).

Q7. Will birds stay at each feeder for less time and make fewer, more targeted visits when feeders are scarce, or will competition drive the opposite pattern?

Prediction: Competition will lead to fragmented, shorter visits (Lanna et al. 2017) and prevent birds from visiting as frequently (Weinstein and Graham 2016), yet birds will maintain high selectivity (Sandlin 2000; Bandivadekar et al. 2018).

Species-level vulnerability

Q8. At the species level, will the breadth of a species' foraging niche (temporal, spatial, or selectivity axes) predict its vulnerability to dropping out under scarcity?

Prediction: Yes: species with broader foraging niches are less vulnerable to resource loss (Lindberg and Olesen 2001; Carscadden et al. 2020).

Methods

Site overview and study species

We conducted all of our experimentation in the dry season of September 2025 at Centro de Investigación Colibrí Gorriazul (hereafter referred to as “Gorriazul”) in Colombia. Gorriazul is situated at roughly 1,700 meters elevation, midway up the western slope of the Eastern Cordillera of the Colombian Andes, in a matrix of pristine rainforest and agricultural properties (4.38168°, -74.35136°). At Gorriazul, there is a well-established network of 16 sugar-water feeders (Fig. 1a) that cover a small area of 154.9 square meters (pairwise distances between feeders range from 0.5–24.2 meters). A longstanding, abundant community of hummingbirds of roughly 10–18 species feeds from both these feeders and many native flowers in the surrounding landscape.

Since 2017, the research team at Gorriazul has been collecting data on nearly 2,000 individual hummingbirds captured onsite (using baited drop-net traps and mist-nets). The majority of these birds have been identified, aged, and sexed based on plumage, bill corrugations, bill serrations, and/or visible brood patches (if applicable), and measured for baseline morphometrics. Over half of these individuals have also been subcutaneously injected with a 35 mg radio-frequency identification (RFID) tag (methods described in Sargent et al. 2026): in our study, these tags comprised 0.31–0.80% of birds' bodyweights (mean 0.56%)—well below the “3–5%” ethical standard applied in most biologging studies (e.g., Wilson et al. 2002; Phillips et al. 2003; Portugal and White 2018). This tagged community provides a rich basis for RFID-enabled, feeder-based behavioral research (experiment described in the following section).

The hummingbirds present and visiting feeders during our experiment ranged considerably in body size and dominance capabilities (Tellez-Colmenares et al. 2025 preprint), representing the following species (arranged in ascending average body mass, as procured from our capture data):

Indigo-capped Hummingbird (*Saucerottia cyanifrons*, 4.97 g), Rufous-tailed Hummingbird (*Amazilia tzacatl*, 5.24 g), Andean Emerald (*Uranomitra franciae*, 5.40 g), Lesser Violetear (*Colibri cyanotus*, 5.53 g), Green Hermit (*Phaethornis guy*, 6.20 g), Brown Violetear (*Colibri delphinae*, 6.86 g), White-vented Plumeleteer (*Chalybura buffonii*, 7.03 g), Sparkling Violetear (*Colibri coruscans*, 8.14 g), and Black-throated Mango (*Anthracothorax nigricollis*, 8.27 g). We also note that there were several Bananaquits (*Coereba flaveola*, 10.9 g) active in the system during this time, which are small, nectarivorous passerines. Hereafter, we will refer to all species by their Latin names (with “Co.” denoting *Colibri* throughout; we use *Coereba* in full to distinguish the two genera).

Experimental overview and inclusion criteria

For this 21-day study, we equipped each feeder with a custom RFID antenna (Fig. 1b), designed at the Humboldt University of Berlin; each unit was furnished with an Adafruit Feather microcontroller, an SD card, and an Adafruit lithium-ion polymer battery (its sole power source), all housed within a watertight snap-lock container. Once hummingbirds were roosting each night, we swapped the batteries with fully charged replacements, downloaded the stored detection data, and returned each SD card to its respective unit. Note that these units operated only from 5:00 AM to 19:00 PM each day, both to conserve battery and given the rarity of nighttime foraging by hummingbirds (Eberts et al. 2019; but see Goertz et al. 1980; Bandivadekar et al. 2018).

Our experiment comprised 7 three-day periods of a mirrored design, in which we progressively removed and reinstated the number of available feeders: A and G had all 16 feeders active; periods B and F had 12; periods C and E had 8; and D, the midpoint, was the period of maximum scarcity with only 4 feeders (Fig. 2). Prior hummingbird research has demonstrated that three days provide a sufficient window for hummingbirds to acclimate to novel feeder configurations (Pimm 1978; Weinstein and Graham 2016). We used a randomizer to select which feeders to remove as soon as periods A, B, and C had ended, and, during each reinstatement phase, we returned the same physical feeders to their original locations (as a means of control and to determine if birds would reestablish preferences or patterns for previously visited feeders). During the course of the experiment, we did not conduct any additional tagging or otherwise manipulate the feeders, which we refilled each evening with identical sucrose solution (approximately 15–20% w/w in concentration).

In our data-cleaning process, we first discarded 51 corrupted rows from the raw RFID logs that were generated by “tag collisions”: when multiple tags enter an antenna’s read field and attempt to transmit data simultaneously, thereby interfering with one another’s signals (Wallace et al. 2020). We next filtered out any sub-second detections (deeming them “quick touches”), retaining only visits with a total duration of ≥ 1 second from first to last detection. We then aggregated consecutive detections of the same individual into a single visit if the inter-detection interval was ≤ 3 seconds; if the gap was > 3 seconds, we treated the succeeding detection as the start of a new visit. On the individual level, our inclusion criteria included: **(1)** birds with ≥ 10 visits in period A, to avoid heavily weighting the effects of scarcity on birds that hardly (or incidentally) used the feeders even in times of abundance; and **(2)** species with ≥ 5 individuals after this period A filter—while a low threshold, it allowed us to examine how a greater proportion of the assemblage responded to the experiment, while still maintaining sufficient sample sizes for our species-level estimates to converge in our mixed-effects models (Bolker et al. 2009).

After filtering, we retained 109 individuals that spanned *Saucerottia cyanifrons*, *Amazilia tzacatl*, *Colibri cyanotus*, *Colibri delphinae* ($n = 6$, which we retained with caution), *Chalybura buffonii*, and *Anthracothorax nigricollis*. Ultimately, we dropped the covariates of sex and age from our analysis: *S. cyanifrons* and *Am. tzacatl* are sexually monomorphic and are therefore impossible to sex with surety via plumage (leaving many of our individuals characterized as “unknown”), and there were only a handful of juveniles ($n = 7$ pre-filtration, $n = 5$ post-filtration) visiting the feeders during our experiment.

Metric definitions

All metrics are italicized upon first introduction in the text. We conducted all analyses in R version 4.4.1 (R Core Team 2022). Throughout the manuscript, we use the terms “removal arc” to signify periods A–C, “reinstatement arc” to signify periods E–G, “baseline” to refer to period A, and “peak scarcity” or “bottleneck” to refer to period D.

Daily basic and transition metrics. For each individual bird on each day of the experiment (henceforth referred to as a “bird-day”), we calculated or extracted the following variables: total *visit count*, total *time* at feeders, *mean visit duration*, unique *feeders visited*, and *present-or-absent* (a binary category, with 0 indicating that the bird had visited at least once on that day, and 1 indicating that the bird had not and was therefore absent from the system). From sequential visits from each bird-day, we also calculated *switch rate* (the rate at which a bird would switch to a different feeder, rather than returning to or remaining at the same feeder from its preceding visit) and *return-given-switch* (the proportion of switches that a bird made to a feeder it had already visited earlier that same day). Next, we calculated two visitation metrics based on Shannon entropy (Shannon 1948; Brereton and Fernandez 2022): *transition entropy*, to assess how varied a bird’s feeder transitions were, based only on the immediately preceding feeder (e.g., Feeder 01 to Feeder 02); and *feeder-use entropy*, to assess how spread out its visits were, based on the proportions of visits that it made to each of the available feeders each day (regardless of order). We normalized both of these entropy measures from 0–1 (with 0 being total predictability and 1 being maximum uncertainty). Additionally, we classified each of these bird-day metrics as occurring on day 1, 2, or 3 of each respective period, in order to test for within-period patterns.

Feeder preference metrics. We next calculated *favorite feeder proportion*: the proportion of visits that a bird made in a single day to its most-visited feeder (see Weinstein and Graham 2016, who used proportion of time at a focal feeder as a similar metric in Andean hummingbirds).

Feeder preference stability. To calculate stability of feeder preferences, we first compiled a daily vector of each bird’s visit counts across all 16 physical feeder positions (setting removed and unvisited feeders as zeroes), then determined how similar those daily vectors were to one another via pairwise Spearman’s rank correlation (similarly applied in Magnhagen et al. 2014; Ward-Fear et al. 2018). We only compared days with identical feeder availability, calculating the average coefficient for each period (*within-period stability*) and for mirrored periods A vs. G, B vs. F, and C vs. E (*mirrored-period stability*, excluding within-period pairs). Given that Spearman’s ρ ranges from -1 to $+1$, we Fisher-z-transformed (Zar 2007) these correlation values to an unbounded scale in order to stabilize the variance and meet our linear-model assumptions (as in Nelson and Mooney 2025). We next calculated *transition matrix similarity*, the cosine similarity between flattened (vectorized) daily transition probability matrices (similarly applied in Gelardi et al. 2019). These two analyses were complementary in that preference stability captures whether birds used the same feeders, while transition matrix similarity captures whether birds used them in the same order.

Feeder-level community metrics. Here, we treated each feeder as the unit, rather than the bird. We first calculated *top-claimant retention*, a binary metric categorizing whether a feeder had received the most visits from the same individual bird in both halves of a mirrored-period pair (0 if no, 1 if yes). We next calculated *similarity of visitor sets*, the Jaccard overlap between two periods' visitor pools (similarly applied in Chung et al. 2019), which we set as (birds visiting both periods) / (birds visiting at least one of the two periods). Lastly, we calculated *visitor distribution similarity*, constructing vectors of how many total visits each bird made to a given feeder across a full period, then calculating the cosine similarity between periods. These two similarity metrics were also complementary: the former captures whether the same birds visited (presence/absence), and the latter captures whether or the same birds visited in similar proportions (counts).

Access hierarchy. We next calculated *relative access*: the proportion of feeder time that each bird had on a given day across all of the detected individuals (cf. Rousseu et al. 2014, who quantified hummingbird monopolization through feeder visit/time data). We used birds' period A averages of daily total feeder time for two additional metrics: **(1)** *scaled period A rank*, which was simply each bird's mean rank in period A, rescaled to 0–1 (with 0 being highest access and 1 being lowest); and **(2)** access tertiles, wherein we classified birds into low-, mid-, and high-access levels, which we treated as a fundamental baseline covariate in our downstream analyses. Finally, we classified birds present in period G but absent in period A as behavioral “recruits” (since we did not tag any new birds during the experiment itself).

Time-niche metrics. For each bird-day, we recorded the timestamps of an individual's *first* and *last visits* (similarly to Calder 1975), from which we calculated *activity span* (the hours between these two timestamps, as a measure of the size of birds' foraging windows). We also used the *suncalc* package (Thieurmél and Elmarhraoui 2022) to produce daily sunrise/sunset times at Gorriazul across the experiment. For our descriptive statistics, we defined a “feeder-hour” as each hour that each available feeder was accessible to hummingbirds, with a maximum of 14 diurnal hours each day (5:00 AM to 19:00 PM, the first and last hour, respectively, in which individuals were registered across the experiment). From there, we calculated *active feeder-hours*: the daily total and proportion of possible feeder-hours (number of feeders × 14) with at least one logged visit, which we then averaged for each period.

System crowding. We calculated *traffic pressure*, the total number of visits made to each feeder, summed across all birds, as a daily measure of hummingbird throughput. In order to separate actual changes in traffic from the methodological artifact of removing feeders (assuming the same number of visits get funneled to fewer feeders, traffic pressure should spike during scarcity by default), we also calculated an availability-scaled version by dividing traffic pressure by the number of feeders offered on each respective day. Next, we calculated *competition inequality*, the Gini coefficient of total feeder time across birds. This metric differs from relative access in that it measures inequality on a scale of 0–1 (similarly applied in Tenczar et al. 2014; Rotics and Clutton-Brock 2021), with 0 being entirely even feeder time across birds and 1 being all the feeder time monopolized by a single bird. Given that there were many hummingbirds at Gorriazul that were untagged but still visiting the feeders, both of these crowding metrics are underestimates.

Bird-experienced crowding and partitioning indices. Finally, we created metrics to test for active partitioning (i.e., birds timing their visits to avoid crowds). To do so, we measured crowding from the bird's perspective, rather than that of the feeder (as described above). For each bird-day, we first calculated *observed crowding*: the average number of tagged birds that were detected at the same feeder within the same 30-minute bin (excluding the focal individual), providing an average

of how many “neighbors” a given bird shared its feeders with. Adapting from Castro-Arellano et al. (2010), we next built a null model against which to compare this observed crowding—*null spatiotemporal expected crowding*—wherein we randomized both the feeder and timing of each bird’s visits across its active window. From these two components, we lastly calculated the *spatiotemporal partitioning index* for each bird’s daily experience: the difference between null – observed, with positive values being less crowding than expected (avoidance), values near zero being crowding levels indistinguishable from the null expectation, and negative values being more crowding than expected (clustering at crowded feeder-times). Here, the partitioning index was robust to the fact that not all individuals at Gorriazul were tagged, given that both observed and null crowding were underestimated in the same way.

Statistical approach

Using the *lme4* (Gaussian and binomial families; Bates et al. 2015) and *glmmTMB* (beta family for proportion responses; Ferrari and Cribari-Neto 2004; Brooks et al. 2017) packages, we fit a series of models that included ordinary linear models, as well as general and generalized linear mixed-effects models with a random effect of bird identity. For most questions, we had a candidate set of 9–10 models: null (random effect only), period only, and additive and interactive combinations of period, species, and access tertile; where appropriate (see per-question analyses below), we substituted mirror-group (A vs. G, B vs. F, and C vs. E) or day-of-experiment (1–21) for period. We note that period and day-of-experiment were too collinear ($r > 0.97$) to include as separate predictors in the same models; we elected to retain the former as our principal predictor, given our experimental design. Aside from day-of-experiment, all variables were categorical: period (7 levels: A, B, C, D, E, F, or G), mirror-group (3 levels), species (6 levels), and access tertile (3 levels: low, mid, or high).

In order to conduct model selection with Akaike’s information criterion (AIC, or denoted as AICc when corrected for small sample sizes), we fit our candidate models using maximum likelihood—since Restricted Maximum Likelihood (REML) is not comparable across models with different fixed effects—and considered any model within $2 \Delta AIC$ of the top-supported model competitive. We then refit our final models with REML to obtain unbiased estimates of the variance parameters. Where relevant (see per-question analyses below), we ran a post-hoc test with our final model, adding day-within-period both as an additive term and as an interaction with period, to determine whether it would improve the fit (similar to the approach in Trigo et al. 2022); we also treated this variable as categorical (3 levels: 1, 2, or 3).

Using the *emmeans* package (Lenth 2021), we extracted estimated marginal means (EMMs, model-adjusted estimates of the response for each level of predictor variable) and contrasts (differences between EMMs) from our top-supported models. For mirrored-period contrasts (A vs. G, B vs. F, and C vs. E) and tertile contrasts (low/mid/high-access), we did not adjust p-values for multiple comparisons, considering the inflation risk of false positives to be minimal with only three contrasts per set; for species pairwise contrasts, however, we applied a Tukey Honestly Significant Difference (HSD) test to control for the error rate across the 15 pairs of our 6 species (as in Duque et al. 2020). Finally, we used the *DHARMa* package (Hartig et al. 2024) to check for the most appropriate model error structure through uniformity, dispersion, outlier, and quantile deviation tests; we also assessed the structure and distribution of our residuals with QQ-normality and residual vs. fitted-value plots.

Per-question analyses

Q1: Competition under scarcity

We assessed competition under scarcity using two metrics: log-transformed, availability-scaled traffic pressure; and competition inequality. Here, our unit of analysis was the whole site of Gorriazul on a single day ($n = 21$ days). As we had only one observation per day (making random effects inapplicable) and continuous dependent variables, we modeled both metrics using ordinary least squares (OLS; Zar 2007), with period as the predictor. We tested day-within-period as an additive term only (we could not test for an interaction with just one observation for each period-day combination). Note that for figure annotations, we fit log-transformed traffic pressure at the feeder-day level ($n = 222$: one row for each active feeder per day, rather than one row per day for the whole site) but displayed raw values for interpretability. Refer to supplementary section S1 for a discussion of two related system-level crowding metrics, which we excluded from the main text given their strong correlation with traffic pressure.

Q2: Access hierarchy stability and body mass effects

Access hierarchy stability. Here, we tested whether relative access was a stable trait across the experiment, fitting a beta generalized linear mixed model (GLMM) on bird-days for which the individual had a relative access score greater than 0 ($n = 1,765$ bird-days across 109 birds). We tested day-within-period as both an additive and interactive term in this case. To compare the A vs. G experimental “bookends” directly, we calculated Spearman’s rank correlation coefficients for each bird, examining whether their mean relative access at the start predicted their mean relative access at the end. We ran this test two ways: on the 81 birds active in both periods; and on the full period-A sample ($n = 109$), assigning any dropouts a value of 0 in period G for their absence.

Body mass and access. Across our six retained species, the tagged birds in our experiment ranged from 4.38–9.28 g. To test whether or not body mass predicted feeder access, we ran complementary tests on three distinct windows: period A (the baseline that we used to define tertiles, $n = 108$ birds with body mass data); period D (peak scarcity, $n = 85$); and the full experiment, averaged across periods ($n = 108$). For each of these windows, we calculated: **(1)** a Spearman’s rank correlation between body mass and mean relative access for each bird (this test pooled inter- and intraspecific variation, as species was not held constant), **(2)** a likelihood-ratio test of whether body mass improved the fit of a species-only OLS model of mean relative access (with the control for species, this model isolated the intraspecific variation), and **(3)** the body mass coefficient and its standard error from the aforementioned OLS. Lastly, we tested whether body mass predicted feeder access differently across periods by fitting a Gaussian LMM of birds’ mean relative access per period ($n = 634$ bird-periods across 108 birds), comparing a period*weight interaction term against an additive alternative via a likelihood-ratio test. Note that here we could not test for day-within-period effects (only one row per bird per period) or the interspecific relationship between body mass and access: with just six species, mass and species identity are effectively confounded, and any pattern ostensibly related to mass could equally have been driven by some other species-level trait that covaries with mass (e.g., bill morphology, position in the dominance network, foraging strategy). A greater number of species would be necessary to explore interspecific mass effects.

Q3: Dropout across experiment

We used our binary present-or-absent metric to identify “dropout” birds that had absences for any days of the experiment. We note that, with this RFID-based metric, we cannot differentiate between birds present at Gorriazul but not visiting the feeders (whether by choice or by exclusion) and birds that had left the area entirely. Because we were interested in how dropout probability varied

continuously with baseline access, we used our scaled period A rank metric rather than our three discrete tertiles. We then fit a binomial GLMM that encompassed all 109 birds on all 21 days ($n = 2,289$). The two models that performed best as per AICc—both of which included an interaction between period and species—were quasi-separated: no individuals from *Co. delphinae* or *S. cyanifrons* had any absences during period A, leading to period*species coefficients that diverged towards negative infinity and standard errors > 40 . We thus proceeded with the third-best model, which did not include a period*rank interaction and therefore had just a single estimate of rank effect across the whole experiment; as such, we could not directly test the relationship between scarcity and access-based dropout—only whether low-ranked birds were more likely to be dropouts overall. As we were more interested in dropout trajectories across the full experiment than within periods, we did not test for day-within-period effects in Q3.

Q4: Preference and visitation reestablishment in mirrored periods

Note that we did not test for day-within-period in our Q4 analyses, since each response variable below (within-period stability, mirrored-period stability, transition matrix similarity, and feeder-level community turnover) was aggregated above the day level.

Feeder preference stability. To determine if birds had consistent feeder preferences across the experiment, we fit Gaussian linear mixed models (LMMs) with our two stability metrics: within-period stability ($n = 591$ across 104 birds) and mirrored-period stability ($n = 245$ across 93 birds). For the sake of interpretability, we elected to back-transform these model effects from Fisher-z to the correlation scale, and we report them like so in our results. We note that one limitation of Spearman’s rank-order correlation is that it is sensitive to the amount of items being ranked (in our case, the number of available feeders) because a misplaced rank can have a disproportionate effect when the number is small—i.e., random pairs of bird-day vectors are more likely to produce high correlations just by chance. To account for this sensitivity, we built a permutation null (a “pre-network permutation” as described by Farine and Carter 2022): for 1,000 replicates, we randomly reassigned each bird-day’s visits to that period’s available feeder set (preserving the bird’s daily visit count and rank structure, but removing its preference signal) and recalculated our stability metrics (as similarly applied in Aplin et al. 2015). We then interpreted all results as the difference between observed – null values, rather than just observed p . Refer to supplementary section S2 for a discussion of an availability-corrected *preference index* that we calculated as well, but ultimately excluded from the main text given its strong correlation with a multivariate feeder-fidelity axis that we use in Q6 and Q8.

Transition  matrix similarity. As with preference stability, we examined transition matrix similarity across the experiment with Gaussian LMMs (standard candidate set), this time fitted only on within-period similarity at the bird-period level ($n = 516$ across 101 birds). To account for differences in feeder availability—fewer options lead to fewer possible transitions, leading to mechanically higher transition similarity—we retained period as a variable in these models.

Community turnover at the feeder level (A vs. G). To assess whether each feeder’s visitor pool remained consistent (as opposed to individual preferences), we focused on three metrics: similarity of visitor sets, visitor distribution similarity, and top-claimant retention. Here, we elected to compare periods A and G, as they each had the full set of 16 feeders and bookended the experiment. We built a permutation null (1,000 replicates) for each of the three metrics, permuting observed bird-feeder associations within each period (while still preserving each feeder’s and each bird’s total number of visits over the period), then calculated two-sided empirical p -values to test whether

the observed and null values differed (cf. Aplin et al. 2015; Farine and Carter 2022). Additionally, we examined the negligible contribution of behavioral “recruits” to turnover, which we report in the supplementary section S2.

Constrained-availability null for system-level behavioral consistency. In order to complement our test of individual preferences on the system level, we assessed whether the across-period variance for our two entropy metrics—feeder-use and transition entropy, both of which we normalized—exceeded that which would arise from random use of the available feeders. Across 1,000 simulations, we reassigned each visit’s feeder by drawing randomly from that period’s available feeder set, while preserving each bird’s daily timing and number of visits (cf. Aplin et al. 2015; Farine and Carter 2022). To aggregate to the system level, we calculated these entropies for each bird-day on the shuffled data, found the bird’s average for each period, then the period average across all birds, and finally calculated variance across the seven periods as our test statistic. We compared our observed across-period variance to our null distribution via two-sided p-values (the proportion of simulations that produced a value different from that observed) and z-scores (similarly to Castro-Arellano et al. 2010). We note here that other metrics (competition, access hierarchy, and dropout) would be invariant to reassigning feeder identity in this way, so we did not apply this method to them.

Q5: Time niches and temporal partitioning

Time niche metrics. We fit Gaussian LMMs on our three time-niche metrics, across $n = 1,765$ bird-days: activity span (hours), first-activity time (minutes after sunrise), and last-activity time (minutes before sunset, which we reflected so that larger values would indicate later end-of-day activity). Distributional transformations did not improve our diagnostics, so we modeled all three metrics on their respective raw scales. As a sensitivity check, we refit our models on a more conservative dataset: for first-activity time, only bird-days with at least one visit before noon ($n = 1,426$, to avoid counting evening visits in this window); for last-activity time, only bird-days with at least one visit after noon ($n = 1,692$, to avoid counting morning visits in this window). For each of our three metrics, we also tested day-within-period as both an additive and an interactive term with period.

Test for active temporal partitioning. We fit Gaussian LMMs on our two crowding metrics—observed crowding and the spatiotemporal partitioning index—across $n = 1,765$ bird-days from all 109 birds, using the full 10-model candidate set (including day-within-period as additive and as an interaction with period). We tested four contrasts here: the three mirrored-period comparisons (A vs. G, B vs. F, C vs. E); and a baseline-vs.-bottleneck comparison (A vs. D), to capture crowding at its maximum. As another sensitivity check, we refit both models on more conservative, midday dataset: only visits at least 90 minutes after sunrise and at least 90 minutes before sunset (42,905 of 59,182 visits, retaining 95% of bird-days), to ensure that our results were not being driven by birds crowding unavoidably near dawn and dusk simply due to circadian or energetic demands. We report this sensitivity check in supplementary section S3.

Q6: Foraging strategies and individual repeatability

Foraging strategy via PCA. Adapting from Falk et al. (2025 preprint), we used a PCA to identify independent axes of variation in hummingbird foraging through six daily metrics: visit count, mean visit duration, switch rate, return-given-switch, normalized feeder-use entropy, and favorite feeder proportion (we tested but ultimately removed a seventh metric that strongly correlated with feeder-use entropy; see supplementary section S4). We excluded one bird from our PCA (a *Colibri*

delphinae that only used one feeder throughout period A and therefore had undefined switching metrics), leaving us in total with $n = 108$ birds and $n = 1,520$ bird-days in our foraging strategy analyses. While only PC1 (42.6%) and PC2 (27.7%) had eigenvalues > 1 and thereby met the Kaiser criterion (Kaiser 1960), we elected to retain PC3 (14.2%, eigenvalue 0.85) for interpretability. Together, the three PCs (which we interpreted as encompassing feeder fidelity, visit frequency and revisitation, and visit duration, respectively) explained 84.5% of variance. As a sensitivity check, we used the Hopkins statistic (Hopkins and Skellam 1954) and k-means clustering (testing for 2–6 clusters; Rousseeuw 1987) to determine if birds formed discrete clusters, with and without four outlier birds with extreme PC scores. Lastly, we modeled each PC score with the standard candidate set of Gaussian LMMs, including both day-within-period tests.

Individual repeatability. We next investigated how repeatable birds were on each PC axis, based on their average scores for each period ($n = 594$ bird-period means across 108 birds, median 7 periods per bird). Using the *rptR* package (Stoffel et al. 2017), we derived intraclass correlation (ICC) coefficients—how much of the total population’s variance is explained by differences between individuals (Nemiroff and Despland 2007; Bell et al. 2009; Gwet 2014)—from the between- and within-bird variances of our LMMs. We fit two simplified Gaussian LMMs on each PC axis: an “adjusted” model that included the random effect of individual and the fixed effect of period, and a null “unadjusted” model that included only the random effect of individual (by subtracting the two’s ICC coefficients, we could quantify how much changes at the period level inflated the apparent within-bird variation). We then bootstrapped 95% CIs (1,000 replicates) and tested the significance of the random effect of individual with a likelihood-ratio test. After this, we characterized the repeatability within other hummingbird groups by separately rerunning the models on each of the three access levels and each of the six species (bootstrapping 95% CIs for each as before, but obtaining p-values for the random effect through 1,000 permutations). With the same adjusted-vs.-unadjusted approach, we also estimated repeatability of activity span at the bird-period level ($n = 641$) and at the bird-day level ($n = 1,765$). See supplementary section S4 for an additional analysis of individual variability, wherein we calculated each bird’s standard deviation in PC1 across periods. Furthermore, note that we did not test for day-within-period effects with our simplified models here.

Q7: Foraging adjustments under scarcity

To determine how birds would alter specific components of their visitation patterns under scarcity, we employed the same dataset as in our Q6 PCA analyses ($n = 1,520$ bird-days across 108 birds) and modeled the primary representative metric that contributed the most to each of the three PCs: favorite feeder proportion (beta GLMM; because beta regression cannot handle exact zeroes or ones, we adjusted any values of 1 to 0.999 and any values of 0 to 0.001), daily visit count (log-transformed, Gaussian LMM), and mean visit duration (log-transformed, Gaussian LMM). For each metric, we included both day-within-period tests. While we considered testing whether travel costs had an effect on visit duration, we ultimately did not include pairwise distances between available feeders in our model given the small differences across periods (mean 6.4–9.9 m).

Q8: Niche breadth and dropout by species

In order to test whether species with greater niche breadths would be less vulnerable to our imposed environmental disturbance (Lindberg and Olesen 2001; but see Carscadden et al. 2020), we selected three axes from earlier questions: *feeder selectivity* (PC1 from Q6’s foraging strategy PCA, wherein higher values represent concentration on fewer feeders; i.e., a narrower selectivity),

temporal niche (activity span from Q5, wherein shorter spans represent a narrower temporal niche breadth), and *movement regularity* (within-period transition matrix similarity from Q4, wherein higher values represent more consistent feeder-to-feeder transitions across days; i.e., a narrower movement repertoire). We pulled species' EMMs from the top-performing model for each respective question and pulled species' dropout probabilities from the Q3 model, then calculated Spearman's rank correlations between each (inverting activity span so that higher values indicated a narrower temporal niche breadth to match that of the other axes).

While we considered compositing the three axes, they were not strongly correlated with one another (feeder selectivity vs. temporal niche: 0.26; feeder selectivity vs. movement regularity: 0.43; temporal niche vs. movement regularity: 0.26) and we expected them to relate to dropout differently, so we chose not to obscure the signal through averaging. We note here that our statistical power was limited with only 6 species; as such, we interpreted the Spearman's correlations cautiously and descriptively (prioritizing direction and magnitude over significance). Lastly, to confirm that the correlation between activity span and dropout was a true pattern across all our species and not just the result of any one outlier, we ran a jackknife test (Friedl and Stampfer 2006; as similarly applied in Lindsay et al. 2026), recalculating the Spearman's ρ after excluding each of the six species one by one. As we did not fit any models here, day-within-period tests were not relevant.

Results

Sample sizes and descriptive statistics

Across our 21-day experiment, our feeder units logged a total of 72,010 raw, uncorrupted RFID detections from 152 individual hummingbirds. All told, we retained 64,213 (89.2%) of these detections—which we aggregated to 59,182 actual visits for our analyses—and 109 (71.7%) of the individuals: we filtered out 7,797 detections that were shorter than 1 second, 35 birds that had fewer than 10 detected visits in period A, and 8 additional birds that met the activity threshold but belonged to species with too few individuals to support species-level analyses (*Uranomitra franciae* $n = 3$, *Colibri coruscans* $n = 3$, *Coereba flaveola* $n = 2$). One species, *Phaethornis guy*, failed both criteria: only one individual visited the feeders during the experiment, and that bird had fewer than 10 visits in period A. Across the 18 days succeeding period A (periods B–G), 1,454 of the 1,962 bird-days (74.1%) had at least one visit, with the remaining 25.9% representing daily absences (the dropout phenomenon that we analyzed in Q3).

The number of birds actively visiting the feeders on a single day fluctuated throughout the experiment, dropping from a peak of 104 individuals in period A (pre-manipulation) to a low of 67 in period E, and only partially recovering to 74 by period G (despite us having restored all the feeders at that point). Hummingbirds' active feeder-hours, meanwhile, were inversely related to feeder availability, rising from 76% in period A to 98% in period D, then gradually dropping back to 62% in period G (see supplementary Table S1).

Our descriptive statistics for the different access tertiles help anchor much of our remaining analysis. The average time that birds spent at the feeders each day in period A, which we used to define the three levels, were as follows: 199 seconds for low-access birds (means ranging from 11–335), 522 for mid-access (range of 337–683), and 1,130 for high-access (range of 693–3,593). Across the *full* experiment, high-access birds spent approximately 5x more time at feeders, made roughly 4x more visits, and used on average 1.3 more feeders than low-access birds each day

(Table 1). However, the hierarchy exhibited different responses to scarcity and reinstatement: when comparing to period A, mean daily feeder time dropped by period D across the board (low -38%, mid -42%, high -48%), but varied in recovery by period G (low +1.5%, mid -23%, high -43%); see Table 2.

Our six focal species were not evenly distributed across the access hierarchy: while 13 of 18 *Ch. buffonii* were low-access, and 8 of 15 *Co. cyanotus* were high, the remaining species did not fall by majority into any one tertile—indeed, the 6 *Co. delphinae* individuals split perfectly evenly into each (Table 3). Across the full experiment, species' average time at the feeders each day spanned 390–642 seconds, only a 1.6x range (Table 4). Relative to period A, losses in mean daily feeder time varied: the species with the shallowest and steepest drops by period D were *Co. delphinae* (-19%) and *Ch. buffonii* (-63%), respectively, while the species with the greatest and worst recoveries by period G were *Am. tzacatl* (-18%) and *S. cyanifrons* (-47%), respectively (Table S2). *An. nigricollis*, meanwhile, gained access in period E relative to period C (+15%).

Q1: Competition under scarcity

Intensity of competition. The average number of visits that each feeder received during the course of a full day rose from 268 in period A to 626 in period D, then declined to 135 by period G (Fig. 3a). The top-performing model was $\log(\text{traffic pressure}) \sim \text{period}$, with an AICc weight of 0.94; adding day-within-period as an additive term did not improve model fit ($\Delta\text{AICc} = 5.35$). Crowding was significantly higher in period D than in any other period (all $p < 0.0001$, Tukey-corrected), and, when comparing mirrored pairs, was higher across the removal arc than the reinstatement arc ($A > G$, $B > F$, $C > E$; all contrasts $p \geq 0.002$).

Inequality of access. Competition inequality hovered around 0.40 in most periods, but rose as high as 0.45 in period D and 0.46 in period E (Fig. 3b). The top-performing model was $\text{competition inequality} \sim \text{period}$ (AICc weight = 0.89); here, too, adding day-within-period as an additive term did not improve model fit ($\Delta\text{AICc} = 4.30$). When comparing mirrored pairs, inequality only significantly differed at 8 feeders, with fewer birds accounting for a larger share of total feeder time in period E than in period C (A vs. G: $p = 0.80$, B vs. F: $p = 0.68$, C vs. E: $p = 0.0002$).

Q2: Access hierarchy stability and body mass effects on access

Access hierarchy stability. Period-A-derived access tertiles strongly predicted relative feeder access across the experiment (Fig. 4). The top-performing model was $\text{relative access} \sim \text{period} * \text{species} + \text{access tertile} + (1 | \text{individual})$, with $\Delta\text{AIC} 11.96$ over the next-best option and highly significant access tertile and period*species terms ($p < 0.0001$); neither test of day-within-period effects improved model fit. Through our diagnostics, we determined that the residuals deviated from uniform distribution and had more outliers than expected (though the dispersion test was not significant). As such, we report the following EMMs and contrasts with caution: on an average day, low-access birds each accounted for 0.36% (95% CI: 0.30–0.42%) of total feeder time across the assemblage, while mid-access birds accounted for 0.91% (0.79–1.05%), and high-access birds accounted for 1.69% (1.48–1.93%)—a 4.7x difference between low and high (all three tertile contrasts on the logit-scale: $p < 0.0001$). Averaged across periods, no species pairs remained significant after the Tukey correction—with shares ranging from 0.61% (*S. cyanifrons*) to 0.91% (*Co. delphinae*), a 1.5x difference—but periods D, E, and G had 5, 3, and 2 significant species pairs, respectively (D: all $p \geq 0.019$, E: all $p \geq 0.025$, G: both $p \geq 0.035$), which reflected *S. cyanifrons* and *Am. tzacatl* receiving less relative access than other species (and *S. cyanifrons* receiving less than *Am. tzacatl* in period G).

When comparing the three mirrored pairs, mean relative access was only significantly higher in period G than A ($p = 0.0003$), likely due to the dropout effect examined in Q3; neither B vs. F, nor C vs. E, were significant (both $p > 0.6$). This result was complemented by our Spearman's rank correlation test, which showed that relative access at the start of the experiment was strongly correlated with relative access at the end of it, both with ($\rho = 0.54$, $n = 109$, $p < 10^{-9}$) and without ($n = 81$, Spearman's $\rho = 0.59$, $p < 10^{-8}$) the 28 birds that had dropped out in period G.

Body mass and access. When capturing the combined effects of inter- and intraspecific variation, body mass and mean relative access were uncorrelated: Spearman's ρ values ranged from -0.11 in period A ($n = 108$, $p = 0.26$), to $+0.09$ in period D ($n = 85$, $p = 0.43$), to -0.02 across the full experiment ($n = 108$, $p = 0.84$). When isolating the intraspecific effect through the species-only OLS model, however, body mass did in fact improve the model fit for period A—with heavier individuals obtaining less relative access at baseline on average ($\beta = -0.004 \text{ g}^{-1}$ relative access, $\text{SE} = 0.001$, $p = 0.005$)—but not for period D at maximum scarcity ($\beta = -0.001 \text{ g}^{-1}$ relative access, $\text{SE} = 0.002$, $p = 0.68$) or across the experiment at large ($\beta = -0.003 \text{ g}^{-1}$ relative access, $\text{SE} = 0.002$, $p = 0.13$). The LMM confirmed that the intraspecific effect of body mass varied across periods: *relative access* $\sim$ *period*weight* + *species* + (*1* | *individual*) outperformed the additive alternative (likelihood-ratio test $\chi^2 = 16.10$, $\text{df} = 6$, $p = 0.013$, $n = 634$ bird-periods across 108 birds).

Q3: Dropout across experiment

The rate of daily absences rose steadily from 4.9% in period A to 38.5% in period E (Fig. 5; see supplementary Figs. S1 and S2 for individual attendance heatmaps and trajectories, respectively). Here, the best-performing model that was not quasi-separated was *absence* $\sim$ *period* + *scaled period A rank* + *species* + (*1* | *individual*), with baseline access rank strongly predicting dropout (access rank coefficient 7.57, $p < 0.0001$). Averaged across periods and species, model-predicted absence probability was 0.07% (CI: 0.01–0.34%) for top-ranked birds, 2.8% (1.2–6.4%) for median-ranked birds, and 55.7% (26.0–81.9%) for bottom-ranked birds—an 800x difference between top and bottom. The dropout probability for a median-ranked bird began at 0.12% in period A, rose as high as 19.2% in period E, and only partially recovered to 9.9% in period G. When comparing mirrored pairs, model-predicted absence was significantly lower across the removal arc than the reinstatement arc ($A < G$, $B < F$, $C < E$; all $z > 5.8$, all contrasts $p < 0.0001$).

For species, predicted absence probabilities ranged from 0.16% (*Co. delphinae*) to 18.0% (*S. cyanifrons*), but only one pair survived the Tukey correction (*S. cyanifrons* > *An. nigricollis*, $p = 0.024$). While *Ch. buffonii* had the highest raw absence rate (33.9%) of any species, this was largely due to its clustering in the low-access tertile: with rank controlled for in the model, *Ch. buffonii*'s predicted dropout was only 3.8%. Conversely, *S. cyanifrons* (raw 27.9%, modeled 18.0%) and *Co. cyanotus* (raw 25.1%, modeled 13.2%) had high model-predicted dropout probabilities for their $\geq 50\%$ clustering in the high-access tertile.

Q4: Preference and visitation reestablishment in mirrored periods

Feeder preference stability. Within-period mean preference stability ranged from 0.69 ρ (period G) to 0.94 ρ (period D). The top-performing model was *Fisher-z(\rho)* $\sim$ *period* + (*1* | *individual*), with an AICc weight of 0.71; access tertile, species, and species*period interactions all failed to improve model fit (all $\Delta\text{AICc} \geq 3.39$). As prefaced, however, this raw ranking is misleading without a permutation null to correct for availability. The differences between observed and null-expected ρ values across the seven periods were as follows: A, 0.86; B, 0.34; C, 0.13; D, 0.07; E, 0.31; F, 0.51; and G, 0.79. Thus, real signal of individual preferences was stronger when the birds had a greater

number of options from which to select. The larger gap in period F than period B (0.51 vs. 0.34), meanwhile, suggests that birds consolidated their preferences after the bottleneck.

For mirrored-period preference stability, the raw mean observed ρ was 0.49 for A vs. G, 0.59 for B vs. F, and 0.72 for C vs. E. Here, *Fisher-z*(ρ) $\sim$ *mirror-group* + (1 | *individual*) performed best (AICc weight = 0.73); again, access tertile, species, and species*mirrored-period interactions all failed to improve model fit (all Δ AICc $\geq$ 2.74). All three mirrored pairwise contrasts were significant, but, consistently with within-period stability, the permutation null inverted rankings. The differences between observed and null-expected ρ values for each of the mirrored periods were as follows: A vs. G, 0.49; B vs. F, 0.18; C vs. E, 0.06. Again, real preserved preference was greater when there were more options.

Transition matrix similarity. For within-period similarity in the daily transitions that hummingbirds made between feeders, *transition matrix cosine similarity* $\sim$ *period* + *species* + (1 | *individual*) was the top-performing model (AICc weight = 0.84); access tertile did not improve fit. Species EMMs ranged from 0.39 (*Ch. buffonii*) to 0.64 (*Co. delphinae*); in our contrasts after the Tukey correction, *Co. delphinae* individuals had greater consistency within periods than both *Ch. buffonii* ($p = 0.013$) and *Am. tzacatl* ($p = 0.046$). Within-period transition matrix similarity did not significantly differ between mirrored periods: A vs. G, $p = 0.42$; B vs. F, $p = 0.56$; C vs. E, $p = 0.11$. For maps of how a representative individual from each species used the available feeders across the experiment, see supplementary Fig. S3.

Community turnover at the feeder level (A vs. G). When comparing between the first and last periods of the experiment, observed turnover at the feeders significantly exceeded that which random reshuffling would produce, with similarity of visitor sets (0.34 observed vs. 0.46 null, two-sided $p < 0.001$) and visitor distribution similarity (0.46 observed vs. 0.56 null, two-sided $p < 0.001$) both falling significantly below their permutation nulls. This was not the case for top-claimant retention: 3 of the 16 feeders had the same primary visitor in both periods, versus the ~ 1.9 expected by chance, a minor difference that was not significant (two-sided $p = 0.13$).

Constrained-availability null for system-level behavioral consistency. Birds did not use the available feeders randomly: across-period variance in both normalized feeder-use entropy and transition entropy fell significantly below their null distributions ($z = -4.77$ and $z = -11.0$ with 1,000 simulations, respectively; both two-sided $p < 0.001$). See supplementary Fig. S4 for the observed values plotted against their respective constrained-availability null distributions.

Q5: Time niches and spatiotemporal partitioning

Time niche metrics. Averaged across all birds, activity span (Figs. 6a, 7a) peaked in period B at 8.55 hours and dropped to a low of 5.59 hours in period E (with 7.94, 6.65, and 6.61 hours for A, D, and G, respectively). *Activity span* $\sim$ *period***species* + *period***access tertile* + *period***day-within-period* + (1 | *individual*) performed best, with the day-within-period interaction greatly improving fit (AICc weight = 1.00, Δ AICc = 50.46 over the next-best). High-access birds had spans ranging from 6.49–10.34 hours, significantly longer than those of low-access birds—which visited feeders across 2.14–4.61 hours each day and compressed those windows under scarcity—in every period (all contrasts $p < 0.0001$). After the Tukey correction for species, only *An. nigracollis* had significantly longer activity spans than *S. cyanifrons* in period A ($p = 0.020$), but species varied more under scarcity: 6 of 15 pairs were significant in period E, with *An. nigracollis*, *Co. cyanotus*, and *Co. delphinae* maintaining relatively long spans, while those of other species tightened. *An. nigracollis* continued to maintain longer spans than *S. cyanifrons* in periods C–G (peaking in D, $p <$

0.001). The day-within-period interaction also revealed that birds progressively contracted their active windows for each additional day of peak scarcity in period D.

Across all individuals, average first-activity time (Figs. 6c, 7c) was earliest in period B at 180 minutes after sunrise and latest in period E at 324 (with 222, 229, and 245 minutes in A, D, and G, respectively). The top model was *first-activity time* ~ *period*species* + *period*access tertile* + *period*day-within-period* + (1 | *individual*), with the day-within-period interaction substantially improving fit once more ($\Delta\text{AICc} = 56.73$). High-access birds started their mornings significantly earlier than low-access birds in every period (all contrasts $p \leq 0.0006$), with the gap largest in period A—high started 278 minutes, or ~4.6 hours, earlier than low—but dwindling across the experiment (155 and 121 minutes in periods D and G, respectively). Post-Tukey, species varied the most in period E (8 of 15 pairs significant), with *Am. tzacatl* and *S. cyanifrons* starting the latest at ~500 minutes after sunrise; in fact, *S. cyanifrons* started consistently later than other species across most of the experiment (significant in 5 of 7 periods). Within periods, birds shifted to earlier start times at the start of the experiment in period A, but did the opposite in period G.

Averaged across all birds, last-activity time (Figs. 6b, 7b) was latest in period A at 44 minutes before sunset and earliest in period D at 126 (with 106 minutes in period G). Here, the best model was last-activity time ~ *period*species* + *period*access tertile* + *period*day-within-period* + (1 | *individual*), with the day-within-period interaction improving fit again ($\text{AICc weight} = 0.88$, $\Delta\text{AICc} = 4.57$). Consistent with the results above, high-access birds ended their evenings significantly later than low-access birds in every period (all $p \leq 0.0012$), but here the gap was largest during scarcity—high ended ~164 min later than low in periods C–D—and smallest in periods A and E (93 and 94 minutes, respectively). With the Tukey correction, species differed in periods B and D–G, primarily reflecting *Ch. buffonii* ending earlier than other species, including *Am. tzacatl* and *An. nigricollis* in periods E–G and *S. cyanifrons* in period E (all $p \leq 0.016$). Within period G at full reinstatement of all feeders, birds shifted to later end times each day.

With the models refitted on our conservative “each-side-of-noon” dataset, high-access birds still had earlier first-activity times in 6 of 7 periods (they no longer significantly differed in period G), and *S. cyanifrons* still started later than other species in 5 out of 7 periods. Yet while high-access birds still had later last-activity times than low-access birds in every period, only 4 species pairs remained significant across all 7 periods after the Tukey correction (compared to 11 in the unfiltered model).

Test for active temporal partitioning. In our test for crowding at feeders from the bird’s perspective, the top-performing model was *observed crowding* ~ *period*species* + *access tertile* + *period*day-within-period* + (1 | *individual*); here, the day-within-period interaction greatly improved fit ($\Delta\text{AICc} = 324.74$ over the additive alternative). The model-estimated average crowding for each period was highest in period D at ~32 other birds per half-hour window at a given feeder, and lowest in period G at ~11. When comparing mirrored pairs, model-estimated crowding was significantly higher across the removal arc than the reinstatement arc ($A > G$, $B > F$, $C > E$; all $p < 0.0001$), and significantly higher by roughly 12.5 birds in the peak scarcity of period D than period A ($p < 0.0001$). Low-access birds experienced significantly more crowding than mid- or high-access birds (both $p \leq 0.018$), while mid- and high-access did not significantly differ ($p = 0.33$). After the Tukey correction, 9 and 6 species pairs remained significant in periods A and B, respectively, with *S. cyanifrons* experiencing the greatest crowding and *Co. delphinae* the least; in periods C–G, only *S. cyanifrons* experienced more crowding than *Ch. buffonii*. Within our removal arc periods A–C, crowding was highest on day 1 and dropped over days 2–3, with the opposite

pattern in periods E–F. See supplementary section S3 for a discussion of the high consistency in results between our unfiltered and midday-only datasets.

In our spatiotemporal partitioning index test of whether the crowding detailed above was greater than would be expected by chance, the best-performing model was *spatiotemporal partitioning ~ period*species + period*day-within-period + (1 | individual)*. Averaged across the experiment, the model estimated that individuals experienced ~5.7 more tagged birds at the same feeder within the same half-hour window than would be expected if both their feeder choices and visit timings had been random across their active windows—in period A, this number was at its highest at ~8, and in period D, it was at its lowest at ~3. When comparing mirrored pairs, clustering relative to random was now significantly greater in A, F, and C than their respective counterparts G, B, and E (all contrasts, $p \leq 0.029$); A also now had significantly more clustering than D ($p < 0.0001$). Post-Tukey, there were 11 and 5 significant species pairs in periods A and B, respectively, driven largely by *S. cyanifrons* crowding the most relative to random and *Co. delphinae* crowding the least; in periods C and onward, there were ≤ 2 significant pairs in any period. Here, the within-period patterns paralleled those that we found with observed crowding. See supplementary section S3 for our midday-only refit, which agreed with the vast majority of these results. We also note that, while a competitive model within $\Delta\text{AICc} = 0.91$ also included access tertile as an additive term (and was otherwise identical), birds from different access tertiles did not significantly differ in their spatiotemporal partitioning (all contrasts, $p \leq 0.099$).

Q6: Foraging strategies and individual repeatability

Foraging strategy via PCA.

PC1 (“feeder fidelity”; Fig. 9a). PC1 explained 42.6% of daily visit variation and was correlated with more heavily visiting a preferred feeder (favorite feeder proportion, 59%), having more predictable feeder usage (normalized feeder-use entropy, –56%), and switching less (switch rate, –53%). The top-performing model was *PC1 score ~ period*species + access tertile + day-within-period + (1 | individual)*, with an AICc weight of 0.98. Averaged across birds, model-estimated feeder fidelity was at its lowest in period B (–0.01) and its highest in period G (0.61), but otherwise ranged from 0.33–0.48 in the other periods. When comparing mirrored pairs, feeder fidelity was significantly greater in G and F than their respective counterparts A and B (both contrasts, $p \leq 0.033$), while C and E did not significantly differ—nor did A and D. Although access tertile improved model fit, high- and low-access birds did not have detectably different levels of feeder fidelity. For species comparisons, however, *Co. delphinae* ($n = 5$) was a strong outlier with high fidelity, differing significantly from as many as four of the five other species in periods C–F after the Tukey correction. Feeder fidelity was, on average, lowest on the first day of each of the 7 periods (0.24), then elevated on the second and third (both 0.46). See supplementary Fig. S5 for our PC1/PC2 loaded biplot.

PC2 (“visit frequency and revisitation”; Fig. 9b). PC2 explained 27.7% of daily visit variation and was correlated with more visits (visit count, 67%), returning to previously visited feeders more often (return-given-switch, 57%), and shorter visits on average (mean visit duration, –44%). Visit duration contributed only moderately here (as per loading thresholds described in Stevens 2002; Hair Jr et al. 2010), but loaded much more strongly on PC3, as described below. The best-performing model was *PC2 score ~ period*species + period*access tertile + period*day-within-period + (1 | individual)*, with an AICc weight of 1.00. Averaged across birds, model-estimated visit frequency and revisitation were at their highest in period B (0.21) and their lowest in period E

(-0.90), then remained low in periods F and G. When comparing mirrored pairs, PC2 scores were significantly greater across the removal arc than the reinstatement arc ($A > G$, $B > F$, $C > E$; all $p < 0.0001$), but A and D did not significantly differ. For this axis, high-access birds had more frequent visits with more revisitation than low-access birds in every period (all contrasts, $p \leq 0.023$). Averaged across periods, no species pairs remained significant after the Tukey correction, but in periods D–G, *An. nigricollis* and *Co. delphinae* visited more often and with higher revisitation rates than numerous other species. In periods B and C, PC2 scores dropped across each of the three days as birds adjusted to the feeder removals.

PC3 (“visit duration”; Fig. 9c). PC3 explained 14.2% of daily visit variation and was strongly correlated with longer visits on average (mean visit duration, 88%), and more weakly correlated with returning to previously visited feeders more often (return-given-switch, 38%) and more visits (25%). This axis largely captured the variation in visit length that was not absorbed by PC2. In this case, the top-performing model was $PC3 \text{ score} \sim \text{period} * \text{species} + \text{access tertile} + \text{period} * \text{day-within-period} + (1 | \text{individual})$, with an AICc weight of 1.00; the day-within-period interaction greatly improved fit ($\Delta AICc = 36.46$ over the additive alternative). Averaged across birds, visits were estimated to be at their shortest in period D (-0.54) and their longest in G (0.09). In mirrored pairs, PC3 scores were only significantly greater in period G than A ($p = 0.032$); in period A, meanwhile, birds had significantly longer visits than in D ($p < 0.0001$). Averaged across periods, low-access birds made significantly shorter visits than mid- and high-access birds (both $p \leq 0.0004$), as did mid-access birds compared to high-access ones ($p < 0.0001$); no species pairs, meanwhile, remained significant post-Tukey. When broken down by period, *S. cyanifrons* made shorter visits than *Am. tzacatl*, *Ch. buffonii*, and *Co. cyanotus* in period E (all $p < 0.04$) and *Co. delphinae* in period D ($p = 0.036$), while *Am. tzacatl* made longer visits than *An. nigricollis* in G ($p = 0.0012$). In periods D and G, visits became progressively shorter across days.

Clustering check. The Hopkins statistic was extremely high (0.996), indicating that the data were not spatially random (Hopkins and Skellam 1954). However, our k-means test indicated that this structure did not equate to distinct clusters: mean silhouette widths in our tests for 2–6 clusters ranged from 0.26–0.33, which all fall into Rousseeuw’s (1987) “weak structure” zone. To determine if this pattern was driven by extreme outliers, we reran the clustering check after excluding 4 birds with $|z| > 2.5$ on any of the PCs ($n = 104$ retained); the Hopkins statistic dropped to 0.885 and silhouette widths remained in the weak structure zone (best $k = 2$, width = 0.334). As such, hummingbird visitation strategies were better described as a continuum along the three PC axes, rather than as discrete behavioral syndromes.

Individual repeatability. Birds were highly repeatable on all three PC axes ($R \geq 0.58$) relative to average behavioral intraclass correlation coefficients (Bell et al. 2009). The random effect of individual identity was highly significant across the board (all three likelihood-ratio test p -values $< 10^{-65}$) and explained 58–72% of variance in each axis after accounting for the effect of period in the adjusted model (PC1 $R = 0.58$; PC2 $R = 0.67$; PC3 $R = 0.72$). Examining the differences between the adjusted and unadjusted models’ ICC values, period effects inflated within-bird variance the most with visit frequency and revisitation (gap of 0.129), intermediately with visit duration (0.045), and the least with feeder fidelity (0.008; most independent of period-level shifts). Low-access birds were less repeatable across PC1, PC2, and PC3 (R values 0.34, 0.29, and 0.30, respectively) than mid- (0.68, 0.64, 0.43) and high-access (0.57, 0.66, 0.79) birds (Fig. 10). Every species was significantly repeatable on every PC, with the exception of *Co. delphinae* on PC1 ($R = 0.16$, permuted $p = 0.085$)—although we note that our permutation tests for that species were

extremely underpowered with only 5 individuals. In terms of magnitude, meanwhile, only *An. nigricollis* ($n = 32$) was strongly repeatable on all three PCs (R values 0.69, 0.67, and 0.68, respectively); while none of the remaining 5 species were consistently less repeatable than the others, each had at least one axis for which R dropped below 0.5. Birds were also highly repeatable in their activity spans on the period level (adjusted $R = 0.78$, 95% CI 0.713–0.825) and the day level (adjusted $R = 0.67$, 95% CI 0.597–0.724).

Q7: Foraging adjustments under scarcity

For the fraction of visits that birds made to their most-visited feeders (Fig. 11a), the top-performing model was *favorite feeder proportion* $\sim$ *period*species* + *day-within-period* + (1 | individual), with an AICc weight of 0.97. Averaged across birds, model-estimated favorite feeder proportions were at their highest in period D at 0.74 and their lowest in period B at 0.62 (0.64 and 0.69 in periods A and G, respectively); when comparing mirrored pairs, birds made significantly more visits to their primary feeder in G and F than their respective counterparts A and B (both contrasts, $p \leq 0.009$), while C and E did not significantly differ. Access tertile did not factor into the top model, but post-Tukey, *Co. delphinae* still had significantly greater top-feeder shares (0.82 mean, 0.92 in period D) than every other species when averaged across periods ($p \leq 0.008$ for all pairs except *S. cyanifrons* with $p = 0.042$). When broken down by period, this signal was strongest in period D, but absent in periods A and B. Across the three days of each period, birds shifted progressively more visits to their favorite feeder (day 1 vs. day 3, $p = 0.004$).

With visit frequency (Fig. 11b), the model that performed best was *log(visit count)* $\sim$ *period*species* + *period*access tertile* + *period*day-within-period* + (1 | individual), with an AICc weight of 1.00 (Δ AICc = 61.52 over the day-within-period additive alternative). As per model predictions, visits made by individuals each day (geometric means, back-transformed from the log scale) were at their lowest at ~ 14 in period E and their highest at ~ 30 in period B (~ 29 and ~ 18 in periods A and G, respectively). In mirrored pairs, birds had significantly fewer visits across the reinstatement arc than the removal arc (A > G by 1.64x, B > F by 1.74x, C > E by 1.66x; all $p < 0.0001$). Mid- and high-access birds visited consistently more than low-access birds across each of the 7 periods (all contrasts, $p < 0.0001$, with high birds making 2.8–4.4x as many visits); indeed, high-access birds also visited significantly more than mid-access ones in periods A–F (all $p \leq 0.014$). With the Tukey correction, *An. nigricollis* and *Co. delphinae* both made more visits than *S. cyanifrons* across the whole experiment (both contrasts, $p \leq 0.011$); by period, 6 of 15 species pairs were significant in periods D and E. Periods B, C, and D had declines in visit count from day 1 to day 2, then a stabilization or partial recovery in day 3.

For visit duration (Fig. 11c), the top model was *log(visit duration)* $\sim$ *period*species* + *access tertile* + *period*day-within-period* + (1 | individual), with an AICc weight of 1.00 (Δ AICc = 77.93 over the day-within-period additive alternative). Model-predicted mean daily visit durations (once again geometric means, back-transformed from the log scale) averaged 15.0 seconds during the removal arc, were at their lowest point in period D at 12.3 seconds, then averaged 17.7 seconds across the reinstatement arc. In mirrored pairs, birds had significantly longer visits across the reinstatement arc than the removal arc (G > A by 1.15x, F > B by 1.18x, E > C by 1.22x; all $p < 0.0001$). Across the full experiment, high-access birds made 1.35x longer visits than low-access birds ($p = 0.0003$) and 1.26x longer visits than mid-access ones ($p = 0.0025$), while low- and mid-access birds did not significantly differ from one another. Only one species pair remained significant after averaged Tukey contrasts: *Am. tzacatl* made longer visits than *An. nigricollis* ($p = 0.002$), a pattern that surfaced more specifically in periods C–G. Additionally, *Co. delphinae* had

shorter visits than 4 other species in period G. While there was no significant change in visit duration across the three days of periods A or D, periods B and C showed increases, and periods E–G showed decreases.

Q8: Niche breadth and dropout by species

Temporal niche strongly predicted dropout (Table 5). Activity span (sign-inverted, so that higher values represent narrower temporal niche breadths) and dropout probability (the model-predicted probability of absence each period) were highly correlated at Spearman's $\rho = +0.829$ ($p = 0.042$). The two species with the longest activity windows, *Co. delphinae* (averaging 7.91 hours) and *An. nigracollis* (averaging 7.33 hours), had the lowest dropout probabilities (0.16% and 0.84%, respectively); the species with the shortest window, *S. cyanifrons* (averaging 4.14 hours), had the highest (17.98%). The rank orderings were otherwise concordant except for *Am. tzacatl*, which dropped out less (3.11%) than its short-to-intermediate activity window (averaging 5.78 hours) alone would predict. With each of the six species omitted in turn via the jackknife test, Spearman's ρ values remained high at 0.70–1.00 (suggesting that no single species drove the correlation), but p -values were 0.188 when we excluded *An. nigracollis*, *Co. delphinae*, or *S. cyanifrons* (which we interpret as power loss due to our small sample of $n = 6$ species, rather than fragility of the underlying trend).

Feeder selectivity and movement regularity, on the other hand, were negatively correlated with dropout but did not significantly predict it (Table 5), with PC1 “feeder fidelity” scores at $\rho = -0.429$ ($p = 0.397$) and transition matrix similarity values at $\rho = -0.143$ ($p = 0.787$). Of the six species, *Co. delphinae* had the highest average PC1 scores (1.75), the highest transition matrix similarity values (0.64), and, as mentioned above, the lowest predicted dropout (0.16%).

Discussion

Our work provides a straightforward experimental design for the study of competitive dynamics between free-living animals that visit artificial resources: progressively removing and reinstating RFID-enabled feeders in a mirrored design (here, $16 \rightarrow 12 \rightarrow 8 \rightarrow 4 \rightarrow 8 \rightarrow 12 \rightarrow 16$) to track visitation patterns under graduated levels of food availability. In our 21-day study in the Colombian Andes, we recorded the feeding patterns of 109 tagged individuals from six representative species that made 59,182 total visits across 1,765 bird-days. Our eight questions assessed hummingbirds' behavioral responses on the following levels: individual (access stability, dropout, feeder fidelity, foraging strategy), species (dropout, niche breadth), and assemblage (crowding and inequality, spatiotemporal partitioning, community turnover). To our knowledge, this is the first investigation to apply RFID technology to such a wide swath of representative hummingbird species, particularly in response to a manufactured resource bottleneck and subsequent recovery.

Q1: Competition under scarcity

Our predictions for Q1 were fully supported. In times of resource scarcity, animals will turn to their remaining options (Boag and Grant 1984), often congregating at them and generating intense competitive conditions (Valeix 2011; Ferry et al. 2016; Delgado-Martínez et al. 2023). As we predicted, our experiment produced exactly such a bottleneck: with 109 individuals funneled onto progressively fewer feeders, traffic pressure surged from an average of 268 total visits to each feeder each day at baseline (period A, with the full suite of 16 feeders) to 626 during peak scarcity (period D, only 4 feeders)—an increase of roughly 2.3x. Nevertheless, hummingbird throughput

failed to recuperate as we restored feeders, remaining lower across the reinstatement arc than every mirrored period of the removal arc (e.g., only 135 daily visits on average to each feeder in period G, roughly half that of period A). This asymmetric recovery is consistent with findings that hummingbirds will respond rapidly to decreases in feeder availability, but return to their former patterns more slowly once those feeders are returned (Pimm 1978); rather than rapidly equilibrate, populations are often more likely to experience long, transient dynamics in response to disturbances (Hastings 2001), including in the foraging behaviors adopted (Karakoç et al. 2017).

Competitive inequality, on the other hand, was greater in the reinstatement arc only at 8 feeders ($E > C$); once we returned to 12 and 16 units, the distribution of feeder time across registered birds was similar to that of the removal arc. A likely explanation for this discrepancy is the dropout effect examined in Q3: dropout was at its peak in period E, with many low-access rivals filtered out and a greater proportion of high-access birds (more prone to gaining disproportionate or exclusive access to the feeders) left active in the system. Resource monopolization is extremely well-documented in hummingbirds (e.g., Grant 1993; Rousseu et al. 2014), and is more favorable when **a**) there is sufficient nectar to support energetically expensive defense (Cotton 1998; Justino et al. 2012; Rousseu et al. 2014; Sargent et al. 2021), but **b**) the territory or resource is not so lucrative that a bird is in constant combat to maintain it (Gill and Wolf 1975; Carpenter 1987). It is possible that the intermediate number of feeders offered in periods C and E, operating in conjunction with widespread dropout, generated especially apt conditions for resource monopolization.

Q2: Access hierarchy stability and body mass effects on access

Our predictions for Q2 were partially supported. We chose to focus on access—the daily feeder time of each bird—as our primary metric of interest throughout this analysis, as it is an objective measure of which individuals can actually acquire a resource, and to what degree, without *a priori* behavioral assumptions. While hummingbird dominance hierarchies provide a useful basis for understanding asymmetric competitive abilities and dynamics by pinpointing the repeated victors (and losers) of aggressive interactions over contested resources (Rodríguez-Flores and Arizmendi Arriaga 2016; Bribiesca et al. 2019; Márquez-Luna et al. 2019), dominance rank is not necessarily interchangeable with access rank: a subordinate bird can still obtain more time at a feeder than a dominant one simply by visiting persistently (Tellez-Colmenares et al. 2025 preprint). However, continuous measures of individual feeder time over a sustained period remain relatively rare in free-living hummingbirds, with research more commonly focusing on short-term time budgets (e.g., Pimm et al. 1985; Powers and McKee 1994) or additional mechanics that underlie access, such as how spatial memory of rewarding feeder locations can positively affect the probability of territory ownership (Araya-Salas et al. 2018) and how sucrose quality can affect the likelihood of resource defense (Powers and McKee 1994; Camfield 2006). In Great Tits, meanwhile, total time spent at RFID-enabled feeders has predicted food consumption and been repeatable across days, as well as been correlated with dominance scores and displacement counts (Cole and Quinn 2011); in this way, access provides a closer proxy for fitness, and we expected it to inform many of the downstream results across the experiment.

We predicted that baseline access would differ across the tagged individuals visiting in period A, and that birds that began as “high access” would remain so, even during times of scarcity and recovery. Average daily access did indeed vary widely in period A, with the extreme ends of the spectrum being as few as 11 and as many as 3,593 seconds (59.9 minutes) of feeder time. With the assemblage stratified into period-A tertiles, low-access birds averaged 3.3 minutes at the feeders

each day, mid-access birds averaged 8.7, and high-access birds averaged 18.8. The relative access of birds at the start and end of the experiment were strongly correlated, and our tertiles predicted access across the study at large: had feeder time been split evenly across all 109 birds, each bird would have received a share of 0.92%; instead, low-access birds received an average share of 0.36%, mid-access received 0.91%, and high-access birds received 1.69%, as per our model estimates—a 4.7x difference. Access was therefore a striking and consistent behavioral trait throughout our manipulation.

While some species skewed towards different levels of baseline access in period A—72% of tagged *Ch. buffonii*, for instance, were in the low tertile, while 53% of *Co. cyanotus* were in the high tertile—the rest were more evenly distributed across the three bins. As prefaced above, these trends in access are not perfectly concordant with interspecific dominance rankings: a free-living study carried out at Gorriazul’s feeders in 2016 (Tellez-Colmenares et al. 2025 preprint) showed that *Ch. buffonii* occupies a mid-to-upper position in the assemblage dominance network, while *Co. cyanotus* ranks lower-to-mid (although we note that the fieldwork for our study was conducted nearly a decade later and advise caution when interpreting this “mismatch”). By peak scarcity, every species averaged less daily time at the feeders than they had at baseline, a loss most pronounced in *Ch. buffonii* (−63%) and least pronounced in *Co. delphinae* (−19%); by full reinstatement, every species had only partially recovered. Interestingly, the most and least complete recoveries belonged, respectively, to *Am. tzacatl* (−18%) and *S. cyanifrons* (−47%), the two smallest and most subordinate species (Tellez-Colmenares et al. 2025 preprint)—both of which had received significantly less access than other species in the periods of greatest scarcity and competitive inequality (D–E). Across the full experiment, our model estimates of each species’ average share of total feeder time ranged from 0.61% (*S. cyanifrons*) to 0.91% (*Co. delphinae*), only a 1.5x spread. Intraspecific variation thus played a greater role in shaping the access spectrum than interspecific variation. This result contributes to a growing body of work suggesting that even a single individual, let alone a species, can exhibit multiple feeder-visitation or foraging strategies within a short span of time (Sargent et al. 2021; Falk et al. 2025 preprint).

We also expected body mass, one of the strongest predictors of dominance in birds (Miller et al. 2017; Francis et al. 2018; Tellez-Colmenares et al. 2025 preprint), to mediate access to the feeders. Larger size confers a physical advantage in combat and has long been tied to interspecific dominance hierarchies in hummingbirds (Dearborn 1998; Justino et al. 2012; Bribiesca et al. 2019; Márquez-Luna et al. 2019; Echevarría and Buitrón-Jurado 2025); however, we could not test the interspecific effect of body mass directly with only six focal species, and therefore focused on the intraspecific effect (albeit more speculatively). Contrary to our expectations, heavier birds within a species obtained slightly less relative access at baseline, although this effect dissolved as the experiment progressed. The most plausible explanation is that lighter hummingbirds merely had smaller energy reserves (e.g., body fat, nectar in their crop or digestive system) and visited more to maximize their nectar intake (Hainsworth et al. 1981; Carpenter et al. 1991; Chin and Lentink 2016; Eberts et al. 2019; Sargent et al. 2026), producing an ostensible “advantage” in period A that could not be sustained under higher competition. Another possibility is that competitive ability simply does not relate to variation in body mass within species as it does across them—intraspecific traits such as age, sex, and individual experience can also contribute to how well a bird accumulates energy (Carpenter et al. 1993). While we cannot distinguish between these two explanations with our data, we *can* surmise that body mass was not a strong mediator of access at Gorriazul at the intraspecific scale.

Q3: Dropout across experiment

Our prediction for Q3 was fully supported. Competitive displacement has been well-documented in hummingbirds (Kodric-Brown and Brown 1978; Altshuler 2006), with dominant individuals or species often expelling subordinates to poorer-quality alternatives (Lyon 1976; Pimm 1978; Pimm et al. 1985; Carpenter et al. 1993; Mendonça and Anjos 2005; Camfield 2006). Indeed, theory predicts that in systems with asymmetric competitive abilities, weaker rivals can be excluded from the resources entirely (Keddy 2001; Łomnicki 2009), a concept that has been borne out in hummingbirds when resource availability is low (Powers and McKee 1994). We thus expected access rank to be a strong driver of feeder absence, with low-access birds more likely to drop out under scarcity.

Daily absence rate rose steadily from 4.9% at baseline (period A) to 38.5% in period E, and dropout probability did indeed vary starkly across the access spectrum, estimated at 0.07% for top-ranked birds, 2.8% for median-ranked birds, and 55.7% for bottom-ranked ones—a range of roughly 800x. Dropout was significantly higher across the reinstatement arc than the removal arc, and only 74 tagged birds were still actively visiting by the final day of the experiment, leaving 35 of the original 109 individuals (32%) unaccounted for; in short, returning feeders did not restore attendance to its baseline levels. With RFID data, we cannot ascertain how dropouts coped when away from our feeders, but when faced with superior competitors or scarcity, hummingbirds have been shown to expand their search areas (Hazlehurst and Karubian 2018), shift to lower-quality resources or sites (Camfield 2006; Lanna et al. 2017), and even subsist on arthropods alone when necessary (Montgomerie and Redsell 1980). For low-access birds that had only been averaging a few minutes of feeder time to begin with, the feeder array may thereby have reached some risk threshold (Hurly 2003) wherein it was no longer worth visiting. As noted in the methods, our models only enabled us to conclude that low-ranked birds were more likely to be dropouts overall; we could not test the period*access-rank interaction directly.

Species, meanwhile, varied widely in their dropout patterns. While *Ch. buffonii* individuals had the highest raw absence rate (33.9%), this was largely driven by their clustering in the low-access tertile: after controlling for rank, *Ch. buffonii*'s predicted dropout was only 3.8%. Predicted absence probabilities across all six species were lowest in *Co. delphinae* (0.16%) and highest in *S. cyanifrons* (18.0%). In fact, *Co. delphinae* had a lower probability of dropping out than we would expect given that its constituents were perfectly split across each of the three access bins, while *S. cyanifrons*' dropout probability was higher (exactly half of its individuals classified as high-access in period A). *Co. cyanotus*, our most consistently high-access species, also had a higher dropout probability (13.2%) than we would expect based on rank alone. Taken together, these results suggest that, while access may have structured the absences of some species, it was not the sole driving force of dropout for all of them. Species-specific traits (e.g., dominance, activity patterns) and strategies likely also mediated dropout or exclusion (Pimm 1978; Pimm et al. 1985; Powers and McKee 1994).

Q4: Preference and visitation reestablishment in mirrored periods

Our predictions for Q4 were partially supported. Hummingbirds can quickly establish preferences for specific resources (Hurly 2003), maintaining both a strong fidelity to them (Bandivadekar et al. 2018) and a remarkable spatial memory of their whereabouts (Healy and Hurly 2013; Araya-Salas et al. 2018), even when they are not actively providing nectar (Gowda et al. 2012). As such, we

expected birds to have preferred feeders that they would visit more consistently and then reclaim during the reinstatement arc, rather than be displaced by newcomers. At the individual level, birds did indeed return to their preferred feeders after the bottleneck. After accounting for chance correlations between daily visit vectors, the real, preserved signal of these preferences was stronger when the birds had a greater number of options from which to select: within periods, retained signal was highest with 16 feeders in A (0.86) and G (0.79), but lowest with 4 feeders in D (0.07); in mirrored periods, it was highest between A and G (0.49), but lowest between C and E with only 8 feeders each (0.06).

Although species did not factor into our preference stability models, they did vary in the daily transitions that they made between feeders within periods: *Co. delphinae*, the species with the greatest overall consistency in feeder-to-feeder transitions from day to day (0.64), significantly differed from *Ch. buffonii* (the species with the weakest overall consistency; 0.39) and *Am. tzacatl*. We expect that hummingbirds with preferred resources—whether through stationary interference, traveling exploitation, or some intermediate point on the foraging spectrum (Gowda et al. 2012; Rico-Guevara et al. 2021; Sargent et al. 2021)—would more readily reestablish familiar feeder-visitation patterns (Tello-Ramos et al. 2015) than those employing more haphazard, opportunistic strategies (e.g., Feinsinger 1976; Sandlin 2000). *Co. delphinae*, which also had the least model-predicted dropout and the greatest multivariate feeder fidelity (Q6), may fit the former profile more aptly; *Ch. buffonii*, with the most raw dropout, the steepest proportional loss in daily feeder time by peak scarcity (Q2), and consistently earlier last-activity times than other species in most periods (Q5), may fit the latter. Across all species, birds were internally consistent when comparing the within-period transition matrix similarity of mirrored periods (e.g., A and G). Access tertile, meanwhile, did not improve the fit of either model, suggesting that any access-driven differences in feeder preference or transition consistency were too small or noisy to register.

At the feeder level, however, turnover between the start and end of the experiment largely exceeded that which random reshuffling of bird-feeder associations would produce: different sets of birds visited the feeders, and the same birds visited to different degrees, although the rate at which feeders retained the same top visitor did not significantly differ from chance. These results together suggest that preference stability across the assemblage was not sufficient to keep the same individuals monopolizing the same feeders. Lastly, at the system level, hummingbirds used the available feeders nonrandomly, with variance across periods in the spread of a bird's visits and the variation in its feeder transitions both falling significantly below their null distributions. One possible means of reconciling these three tiered results—stable individual fidelity to feeders and transitions, unstable feeder visitors, and stable system-wide feeder use—is again the dropout effect examined in Q3: with roughly a third of the original 109 hummingbirds no longer attending the feeders, the visitor pool at each feeder shifted by default, even when the birds that did not drop out generally returned to their original preferences. Avian RFID data have demonstrated elsewhere that it is common for some individuals to contribute disproportionately to a given feeder's visits (Galbraith et al. 2017; Bandivadekar et al. 2018), rendering visitor pools highly sensitive to which birds remain active.

Q5: Time niches and spatiotemporal partitioning

Our predictions for Q5 were not supported. Niche theory posits that competitors may temporally partition their use of shared resources as a means of stably coexisting (Schoener 1974; Kronfeld-Schor and Dayan 2003); in these cases, subordinates adjust their activity patterns to access the

resource only when dominants are absent (Craig and Douglas 1984; Cotton 1998; Lara et al. 2009; Stone et al. 2019; Maziarz et al. 2023), such as during afternoon windows in some hummingbird systems (Antunes 2003). We therefore expected low-access birds to extend their activity windows—rising earlier in the mornings and departing later in the evenings than high-access individuals—in order to obtain sufficient energy from the feeders, particularly under scarcity.

On the contrary, low-access birds significantly diverged from high-access ones in every single period, with shorter spans (2.14–4.61 hours per day vs. 6.49–10.34 hours), later start times (a gap of up to 278 minutes, or 4.6 hours), and earlier end times (a gap of up to 164 minutes, or 2.7 hours) across the board. In fact, as scarcity intensified, *all* birds compressed their activity windows from both ends, even condensing from day to day within period D itself (3.7 → 2.0 → 2.5 hours), reflecting hummingbirds’ ability to rapidly adjust their behavior to changes in nectar availability (Pimm 1978; Garrison and Gass 1999; Hazlehurst and Karubian 2018), and consistent with spatiotemporal niche compression documented in other human-disturbed systems (Gilbert et al. 2022). Interestingly, however, the gap between low- and high-access birds’ first activities shrank across the experiment (121 minutes in period G), but the gap between their last activities widened under peak scarcity (164 minutes in period D). Amongst species, meanwhile, *An. nigricollis* stood out for having generally longer spans than *S. cyanifrons*, which started later than others across most of the experiment, while *Ch. buffonii* ended earlier than both of them (as well as *Am. tzacatl*) in some periods.

Crepuscular hours are of great energetic importance to hummingbirds and are associated with spikes in foraging activity (Wagner 1946; Pearson 1954; Beuchat et al. 1979; Stiles and Wolf 1979; López-Calleja et al. 1997; Bandivadekar et al. 2018). Hummingbirds rapidly deplete their lipid reserves while they sleep (Halter 2026)—even awaking in an energy deficit when they have not consumed enough nectar (Tooze and Gass 1985; Hiebert 1991; Tiebout 1991; Gass et al. 1999)—and must quickly refuel in the mornings; prior to roosting in the evenings, hummingbirds often crop load to accumulate fat and support their overnight metabolism (Powers et al. 2003; Eberts et al. 2019), thereby reducing the need for risky torpor (Shankar et al. 2020). It is possible that low-access birds attempted to visit in these marginal hours and were rebuffed, or simply elected to forage elsewhere in the more competitive windows of the day to avoid combat-induced injury (e.g., Kodric-Brown and Brown 1978); either way, high-access birds visited during these metabolically critical hours, and low-access birds largely did not. This result aligns with the reality that temporal partitioning is rare in animal communities in practice (Schoener 1974; Lara et al. 2011). Moreover, the feeders in our experiment—which have been continuously stocked at Gorriazul each evening for over a decade (Tellez-Colmenares et al. 2025 preprint)—do not meet the typical conditions that favor temporal partitioning, as they do not self-replenish within a single day (e.g., as flowers can), which would otherwise enable a second party to strategically visit after the first had depleted them and vacated the area (Craig and Douglas 1984; Kronfeld-Schor and Dayan 2003).

While activity data showed us that low-access birds did not relegate themselves to more extreme hours of the day, we also guessed that birds might partition on a finer scale, staggering their visits within their own active windows. Yet this was not the case either. In absolute terms, crowding was highest during peak scarcity (period D) at an estimated ~32 rivals per half-hour window at a given feeder (significantly higher than in baseline, period A, by ~12.5 birds), and lowest during the experiment’s end (period G) at ~11. However, the spatiotemporal partitioning index showed that birds packing together in this way was largely an artifact of feeder availability: across the full

experiment, individuals experienced ~5.7 more tagged birds at the same feeder within the same half-hour window than would be expected if both their feeder choices and visit timings had been random, but ~8 (the most) in period A and ~3 (the fewest) in period D. In short, with more feeders, there are far more possible bird-feeder-time combinations, so observed crowding registers more strongly against the null than at peak scarcity, when crowding is more likely regardless of feeder choice or timing. Nonetheless, birds experienced more crowding than would be expected by chance, even during midday alone (supplementary section S3), ruling out the possibility of mere circadian-driven crowding at sunrise and sunset. Low-access birds experienced significantly more absolute crowding than mid- and high-access birds, but did not actively cluster more or less than them under random visitation. For crowding on the species front (both absolute and relative to chance), *S. cyanifrons* experienced the most, and *Co. delphinae* the least, across several periods. Feeders support markedly crowded, contentious conditions (Lanna et al. 2017; Lawson et al. 2018; Manikowska-Ślepowrońska and Ślepowroński 2025), and our system was no exception; this assemblage appears to coexist by partitioning primarily along some niche other than time, such as the competitive displacement discussed in Q3 (Amarasekare 2003).

Q6: Foraging strategies and individual repeatability

Our predictions for Q6 were fully supported. The emerging perspective in ecological literature is that the standard binary classifications of territoriality and traplining oversimplify hummingbird foraging strategies (Altshuler et al. 2004), which, given the highly flexible behavior of these tiny birds in response to energetic and risk landscapes (Kodric-Brown and Brown 1978; Hixon et al. 1983; Stiles 1985; Carpenter 1987; Justino et al. 2012), are more likely to exist on a spectrum (Rico-Guevara et al. 2021; Sargent et al. 2021; Falk et al. 2025 preprint). Despite this plasticity, individuals can be strikingly consistent in their own behaviors (e.g., some individuals are bolder than others), but this repeatability varies depending on the behavior in question (Bell et al. 2009). As such, we expected individuals to fall along a continuum of feeder-visitation space and to retain their own idiosyncratic signatures while modifying their strategies under scarcity, but for some components of their behavior to be more repeatable than others. With our PCA, we characterized individual foraging behavior along three axes, which collectively explained 84.5% of daily visit variation and described “feeder fidelity” (PC1, 42.6%), “visit frequency and revisitation” (PC2, 27.7%), and “visit duration” (PC3, 14.2%).

Birds did indeed form a visit-strategy continuum, as opposed to discrete behavioral clusters. Even *Co. delphinae*—which stood out during scarcity and recovery as having particularly higher feeder fidelity, more frequent visits, greater revisitation, and longer bouts than some other species—lay on the continuum extreme, rather than composing its own cluster. Our work thus joins a growing number of RFID-based studies that have demonstrated spectra in hummingbird feeder visitation: when visiting feeders spaced at least 90 meters apart and spanning > 1 kilometer total, White-necked Jacobins (*Florisuga mellivora*) in Panama exhibited continuous movement characteristics that ranged from territoriality to non-territoriality (via PCA on similar daily movement metrics; Falk et al. 2025 preprint); while Ruby-throated Hummingbirds (*Archilochus colubris*) in Quebec displayed a continuum of strong defense to no apparent defense, according to their fidelity to different feeders over time and the number of visits made by competitors (Rousseu et al. 2014). Notably, our PC1 scores did not significantly differ across access tertiles, suggesting that feeder fidelity here did not necessarily equate to monopolization in the Gorriazul assemblage—perhaps due to the intense competition from Q1 and due to interspecific dynamics that were non-applicable in Rousseu et al.’s (2014) system. Along the other PCs, high-access birds had more frequent visits

with more revisitation than low-access birds in every single period, and on average made significantly longer visits than mid- and low-access birds (while mid-access birds made longer visits than low-access ones). Only *An. nigricollis* otherwise had more visits and revisitation than other species, while *S. cyanifrons* had shorter visits than some, and *Am. tzacatl* had longer ones. Once again, day-within-period effects were significant across each axis, indicating that birds adjusted their foraging strategies both on a daily basis and across periods.

As expected, hummingbirds were also highly repeatable along all three PCs (PC1 $R = 0.58$, PC2 $R = 0.67$, PC3 $R = 0.72$). In fact, they were far more repeatable in their behavior than most animals are, as per average estimates from Bell et al.'s (2009) meta-analysis: $R = 0.37$ across 98 species and 13 categories of behavior, and $R = 0.40$ across 6 species for foraging behaviors specifically (an average we derived from their supplementary materials). The variation in repeatability from axis to axis also matched our predictions, as some types of behavior (e.g., aggression) are more repeatable than others (e.g., activity), while the high overall magnitude may be partially explained by the compressed nature of our experiment (21 days total), for individuals are generally more repeatable over short (< 1 year) periods (Bell et al. 2009). Hummingbirds ultimately retained their individual signatures—in other words, their relative positions in the strategy space—even as the assemblage at large shifted towards greater fidelity, fewer and less revisitation-heavy visits, and shorter bouts under scarcity (e.g., the most frequent visitors remained the most frequent). Our experimental design explained the most variation in visit frequency and revisitation, a medium amount in visit duration, and the least in feeder fidelity, which was the most stable individual trait and the least affected by our periods. Birds also had individual temporal signatures, being highly repeatable in their activity spans on both the period level ($R = 0.78$) and the day level ($R = 0.67$).

Notably, repeatability was not uniform across the assemblage. Low-access birds were less consistent across all three axes than mid- and high-access ones; it is possible that birds with less stable access to the feeders were consequently more haphazard foragers (Feinsinger 1976) that could not establish preferences or routine visitation patterns as easily (or vice versa), or deliberately adjusted their strategies to obtain some measure of time at the feeders when faced with monopolizing competitors (the “necessity drives innovation” hypothesis, as detailed by Cole and Quinn 2011). Of course, birds with more inconsistent strategies may simply have been more likely to drop out (which would align with the low-access dropout seen in Q3), making this result a selective effect and not a behavioral one. Amongst species, only *An. nigricollis*—also consistently one of the most dominant of the assemblage (Tellez-Colmenares et al. 2025 preprint)—was highly repeatable on all three axes.

Q7: Foraging adjustments under scarcity

Our predictions for Q7 were fully supported. Hummingbirds frequently engage in aggressive interactions to physically exclude rivals from resources (Sargent et al. 2021; Tellez-Colmenares et al. 2025 preprint). In crowded systems such as ours (Q5), dominant individuals regularly struggle to maintain their monopoly against the rush of competitors: chasing off one subordinate produces a momentary, undefended window that a second subordinate can take advantage of until being ousted in turn (Lanna et al. 2017). Hence, lower-ranking individuals must often accept repeated displacement as the cost of accessing a resource, while dominants must often interrupt their own bouts to expel intruders if they wish to control it (Lanna et al. 2017)—leaving neither party a long opportunity to feed. We thus predicted that visits would be shorter under scarcity across the board. Presumably, experimentally reducing feeder availability would restrict overall access even further

by funneling more individuals onto fewer options and thereby intensifying competition (as in Q1, Valeix 2011; Ferry et al. 2016; Delgado-Martínez et al. 2023); as such, we also expected birds to make fewer visits under scarcity. Finally, hummingbirds can have strong fidelity to specific flowers and feeders (as in Q4, Gowda et al. 2012; Bandivadekar et al. 2018) and can maintain this selectivity even under high competitor densities, so long as they have complete information about the quality of the nectar (Sandlin 2000). Given that all of our feeders offered identical nectar each day, there was no such information deficit in our system that might spur opportunism (Sandlin 2000), and so we predicted that birds would remain highly selective throughout. Note that while some individuals abandon territorial behavior entirely when competition is too steep (Carpenter 1987; Justino et al. 2012), others do not (Lanna et al. 2017); based on our observations of the Gorriazul assemblage (e.g., Tellez-Colmenares et al. 2025 preprint), we expected these interference dynamics to persist across the experiment.

As we removed units from the array, birds did indeed make shorter, fewer visits that were more concentrated on their preferred feeders each day. From baseline to peak scarcity, visit durations dropped by 20% (15 seconds to 12 seconds), visit counts fell by 52% (29 to 14 per day), and favorite feeder proportion rose by 16% (0.64 to 0.74). In the reinstatement arc, none of these metrics returned to their respective removal arc levels: visits actually lengthened by 15–22%, but remained fewer in number and more concentrated at preferred feeders. This increase in visit duration may reflect the inverse relationship documented in Falk et al.’s (2025 preprint) RFID work, wherein hummingbirds can compensate for reduced visitation by making those visits longer, and vice versa—a pattern also captured by our own PC2 (loadings: visit count +0.67, mean visit duration –0.44). As in Q5 and following from Q6, day-within-period effects were significant for all three metrics, with favorite-feeder proportion rising across days, and, within most removal periods, visit counts declining and visit durations lengthening.

Beyond assemblage-level patterns, our access- and species-based estimates largely reflected those of Q6, simply with greater specificity. High-access birds consistently made 1.35x longer and 2.8–4.4x more visits than low-access birds, as well as 1.26x longer visits than mid-access ones, with significantly more visits than them in all but the final period. Meanwhile, mid- and low-access birds were indistinguishable in their visit durations, but the former made more visits than the latter in all 7 periods. The fraction of visits that birds made to their most-visited feeders, however, did not differ between access tertiles, which parallels our finding from Q6’s PC1. Across species, *Am. tzacatl* made longer visits than *An. nigracollis* throughout the majority of the experiment, while in the very last period, *Co. delphinae* made shorter ones than almost all other species. Averaged across the experiment, *An. nigracollis* and *Co. delphinae* also made more visits than *S. cyanifrons*. As per Q6, *Co. delphinae* individuals unsurprisingly stood out for their fidelity: their share of visits to their top feeder averaged 82% across the experiment—exceeding that of every other species—and rose to 92% at peak scarcity. These values are very similar to the average 87% of visits that RFID-tagged Anna’s (*Calypte anna*) and Allen’s (*Selasphorus sasin*) Hummingbirds made to their most-visited feeder during a study in urban California (Bandivadekar et al. 2018), suggesting that even hummingbirds spanning latitudes, elevations, habitats, and clades can share a primary-feeder strategy, one that is apt to intensify under conditions of scarcity.

Q8: Niche breadth and dropout by species

Our prediction for Q8 was partially supported. For a species to successfully coexist with others, it must often have its own “niche”: that is, it must be ecologically distinct for the given environmental

conditions (Chesson 1991; Chesson 2000). A niche can be defined around numerous axes, including the use of different resources—e.g., food, space, time (Pimm 1978; Stiles 1985; Kronfeld-Schor and Dayan 2003; Tinoco et al. 2017; Carscadden et al. 2020; Rojas et al. 2026)—and has important ramifications for vulnerability: a species with greater breadth along a niche axis (a generalist) should be less susceptible to environmental disturbance than a species with narrower breadth (a specialist), according to both theory and empirical work (Lindberg and Olesen 2001; Devictor et al. 2008; Colles et al. 2009; Clavel et al. 2011; Carscadden et al. 2020; Di Cecco and Hurlbert 2022). As such, we expected species with narrower temporal, feeder selectivity, and movement regularity niche breadths to be more likely to drop out under scarcity.

In fact, this prediction was only true of temporal niche: species with shorter activity spans dropped out much more, with a very strong correlation of Spearman's $\rho = +0.829$. On the other hand, species that were narrower in their feeder selection and feeder-to-feeder transitions from day to day had *less* dropout, but neither of these correlations were significant. Recent work has demonstrated that some niche breadths can better predict avian vulnerabilities than others (Di Cecco and Hurlbert 2022); here, feeder selectivity may have been more indicative of competitive establishment—a bird that consistently uses a preferred feeder is plausibly better positioned to monopolize it (Rousseu et al. 2014; Sargent et al. 2021)—and increased selectivity under reduced resource availability has been well-documented in hummingbirds (Maglianesi, Blüthgen, et al. 2015; Tinoco et al. 2017). A narrow movement repertoire, meanwhile, may have been linked to foraging efficiency, with fewer, regular routes between profitable resources saving a bird cognitive load and the time and energy of searching for alternatives (Tello-Ramos et al. 2015; Tello-Ramos et al. 2019; Sargent et al. 2021). Thus, when predicting the vulnerability of different hummingbirds to feeder scarcity, the identity of the axis in question is of great relevance.

Breaking down temporal niche breadth further is fairly straightforward. *Co. delphinae*, with the longest estimated average activity span of 7.91 hours, had the lowest dropout probability at 0.16% (similar to *An. nigricollis*, with 7.33 hours and 0.84%), while *S. cyanifrons* had the shortest estimated average activity window of 4.14 hours and the highest dropout probability at 17.98%. In fact, the only species with a mismatched rank ordering was *Am. tzacatl*, which had a smaller probability of dropping out (3.11%) than its shorter, intermediate activity windows (averaging 5.78 hours) alone would predict. Despite being subordinate in the Gorriazul assemblage, *Am. tzacatl* individuals are persistent visitors (Tellez-Colmenares et al. 2025 preprint)—which in our data translated to longer overall visits than some other species—which may provide them some manner of buffer during times of scarcity. In general, having a greater temporal niche breadth may afford a bird more opportunities to forage during quiet moments, or to compensate for poor floral rewards in the surrounding landscape or lost access from failed fights earlier in the day, thereby lowering the probability of being fully excluded; along these lines, hummingbirds more flexible in their daily behaviors may be more equipped to handle environmental changes (Shankar et al. 2019).

Limitations and proposed solutions

We faced several limitations inherent to RFID technology in our experiment. The first is undercounts (Hughes et al. 2021): the antennas cannot detect more than one tagged individual visiting simultaneously (Wallace et al. 2020), so we lost roughly 50 detections to corrupted reads; more pressingly, there were many untagged birds also visiting the feeders during our experiment, leaving our results representative of merely a portion of the assemblage (yet still silently affected by the rest of it). The second is that while RFID antennas capture visits, they cannot capture the

agonistic interactions that shape them (e.g., Tellez-Colmenares et al. 2025 preprint), such that we can only make inferences about dominance and territoriality—e.g., how competitive displacement may relate to dropout—rather than demonstrate either directly (a constraint also acknowledged in RFID-based hummingbird studies more broadly; Falk et al. 2025 preprint). To address these restrictions, we collected a parallel dataset throughout the experiment: adapting from the methods of Tellez-Colmenares et al. (2025 preprint), we recorded one “core” feeder that was offered all 21 days of the experiment for three one-hour windows (9:00–10:00 AM, 14:00–15:00 PM, 16:30–17:30 PM) each day. After aligning the RFID records with these videos, we can approximate population-level abundance of tagged and untagged birds alike, as well as individual-level contest dynamics of tagged birds, and then finally extrapolate beyond these specific feeder-hours to assemblage-level responses to our manipulation.

Somewhat relatedly, while RFID antennas offer extremely precise spatiotemporal detections, they do not provide any information beyond their limited detection ranges (Falk et al. 2025 preprint), which are often just a few centimeters. When a tagged bird was absent from our feeders, we had no knowledge of its behavior or whereabouts (as acknowledged in Falk et al. 2025 preprint). The landscape surrounding our array—particularly the property of Gorriazul itself—is home to many native, hummingbird-pollinated flowers. Dropout or not, low- or high-access, individuals may well have been visiting these natural resources to fulfill their energetic requirements throughout the experiment. Thus, our access hierarchy in Q2 only enables us to describe how tagged birds divided the feeders—not the total nectar available. Pollen sampling from captured birds (Betts et al. 2015) and records of hummingbird-flower interactions in the surrounding landscape, such as from censuses (López-Segoviano et al. 2018) or timelapse videos (Weinstein and Graham 2016; Barreto et al. 2025), would allow for a more comprehensive examination of how hummingbirds coped with reduced feeder availability. An additional dimension to this question is whether individuals expanded their home ranges or territories in search of nectar (Hazlehurst and Karubian 2018), otherwise adjusted their movement strategies (Mailly et al. 2025; Rueda-Urbe et al. 2026), or if they abandoned the area entirely. To address this uncertainty, we collected a second parallel dataset: in the week preceding our experiment, we captured 58 of the RFID-tagged individuals that were visiting the feeders, equipped each one with a Bluetooth radio-transmitter, and then tracked its movements across a 300 × 300 meter Bluetooth automated radio-telemetry grid that was centered roughly on the station. Building from previous radio-telemetry work in hummingbirds and other nectarivores (Hadley and Betts 2009; Volpe et al. 2014; Smetzer et al. 2021), we will thereby determine if hummingbirds exhibited flexible movement syndromes in response to our experiment, regardless of whether they were actively visiting the feeders or not.

Longer-term feeder experiments, meanwhile, may more robustly reflect hummingbird behavior over time; how hummingbirds use both flowers and feeders varies substantially across seasons and years (Stiles 1985; McCaffrey and Wethington 2008; Márquez-Luna and Arizmendi 2025). Previous hummingbird feeder experiments have been constructed around three-day windows—either for data collection (Pimm 1978) or acclimation (Weinstein and Graham 2016)—and we did the same for our experimental design, including the period A “baseline” that we used as a basis for describing pre-manipulation access levels. While the effects of access across the experiment were consistently strong, suggesting that this three-day period was sufficient to capture meaningful differences between birds, a longer baseline might be more informative. This would allow researchers to: **(1)** better account for temporal fluctuations in individual behavior (Bell et al. 2009) and varying natural conditions (Robb et al. 2008); and **(2)** directly test whether access reflects an

individual's likelihood of dropping out, through the use of less restrictive inclusion criteria (i.e., allowing some degree of absence in the first period so the GLMM does not quasi-separate) or a repurposed continuous-time survival or capture-recapture model (see Bandivadekar et al. 2018 for a Cormack-Jolly-Seber model of hummingbird RFID detections). Along these lines, longer RFID monitoring post-manipulation, as in studies spanning months and years (Bandivadekar et al. 2018; English et al. 2022; Falk et al. 2025 preprint), would allow for a more thorough investigation of experimental carryover on behavior (Pimm 1978) and whether absent birds remain displaced or return to the feeders in the subsequent days or weeks.

Finally, while our inclusion criteria were as minimal as possible to ensure that we could retain a wide representation of the assemblage while still estimating species-level effects, *Phaethornis guy*, *Colibri coruscans*, and *Uranomitra franciae* nevertheless failed to meet them. Each of these species occupies a distinct position in the assemblage and contributes to its diversity. *P. guy* is a medium-sized hermit that is both a trappiner (Stiles 1975; Stiles and Wolf 1979; Hadley and Betts 2009) and the most subordinate species in the Gorriazul dominance network (Tellez-Colmenares et al. 2025 preprint), and thus visits the feeders very sparingly (Avalos et al. 2012). In contrast, *Co. coruscans* is the second-heaviest and one of the most dominant species in the assemblage (Tellez-Colmenares et al. 2025 preprint), and is considered a quintessential territorialist (Sargent et al. 2021). *U. franciae*, meanwhile, is small, and—differentiating from *S. cyanifrons* and *Am. tzacatl*—uncommon and non-aggressive at the Gorriazul feeders, rarely initiating aggressive interactions (Tellez-Colmenares et al. 2025 preprint). In excluding these three species, we ultimately forewent visitation data from birds that are more extreme in their foraging and dominance strategies, and conceivably would have contributed unique signatures across our eight questions as well. On this front, we also excluded several tagged bananaquits (*Coereba flaveola*) that had visited the feeders during our experiment but failed our inclusion thresholds—leaving a passerine competitor uncharacterized. Repeating this experiment after tagging an even greater proportion of the population might allow for an investigation into all 9 species, thereby capturing a more complete picture of the hummingbird foraging continuum.

Broader implications and conclusions

Maintaining bird feeders is a global pastime and, as what amounts to essentially a “massive ecosystem-scale intervention” (Galbraith et al. 2017), is the subject of ongoing biological and conservation debates (Jones and Reynolds 2008). Artificial sugar-water feeders provide a substantial energetic subsidy to hummingbirds throughout the Americas, offered across residential gardens (Meehan et al. 2020), private nature reserves (Brockmeyer and Schaefer 2012; Ramírez-Burbano et al. 2022), and research stations (Sonne et al. 2016; Sargent et al. 2026), with potentially sweeping ramifications on fitness and behavior (Robb et al. 2008; Galbraith et al. 2017). In our system, we found that feeders were dominated by a small subset of individuals—as has been documented in RFID studies of passerines (Galbraith et al. 2017) and urban North American hummingbirds (Bandivadekar et al. 2018)—with some species faring better than others, while the majority of the assemblage only obtained a small share of the total visit time. When we removed feeders, that share shrank even further. In fact, many low-access birds ceased visiting entirely. Hummingbird assemblages that actively rely on feeders may thus be structured around competitive dominance (Keddy 2001) and “hierarchical filtering”: a buffering mechanism wherein some individuals or subgroups can perform consistently better, more successfully withstanding adverse conditions and providing a “floor” against extinction, while inferior competitors suffer disproportionate losses (Milles et al. 2023). In this way, a sudden drop in feeder availability—and

possibly the irregular provisioning that has been documented across many households (Davies et al. 2012; Mady et al. 2021)—could inordinately affect low-ranking individuals. Such circumstances could have potentially cascading effects on the local pollination services that are so critical (Brockmeyer and Schaefer 2012; Tinoco et al. 2017; Ratto et al. 2018), particularly if the natural resource availability is also low (e.g., due to seasonality; McCaffrey and Wethington 2008; Márquez-Luna and Arizmendi 2025) and the birds cannot compensate even when redirecting all of their foraging to the surrounding flowers. Regardless, feeder scarcity did not lead to equal redistribution here, but rather competitive exclusion (Kneitel 2008).

The partial recovery exhibited across the assemblage is also noteworthy. Our removal of 12 of 16 feeders over a 7-day window (feeders removed on the evenings of days 3, 6, and 9) resulted in wide-scale changes in behaviors that did not return to their previous levels, even once we had returned all feeders to their former positions (on the evenings of days 12, 15, and 18). Dropout was the most pronounced of these effects, with approximately a third of the original visitors unaccounted for by the final day of the experiment. Although feeders are theoretically a steady food source (often stocked each day year-round; Jones and Reynolds 2008), and in hummingbirds can sustain both range expansion (Greig et al. 2017; Alexandre et al. 2025) and unnaturally large populations (Wethington and Russell 2003) while simultaneously attracting birds away from native flowers (Arizmendi et al. 2007; McCaffrey and Wethington 2008; Ramírez-Burbano et al. 2022; but see Brockmeyer and Schaefer 2012; Sonne et al. 2016), the populations that depend on them may be more vulnerable than they appear. Of course, we recognize that feeders are an extreme case in that they are “bonanza” resources (Arizmendi et al. 2007) that are effectively unlimited in a way that natural resources are not (McCaffrey and Wethington 2008; Sargent et al. 2021); nevertheless, it is possible that hummingbird populations reliant on flowers would also be slow to recover under natural variation or scarcity, such as due to climate warming (McKinney et al. 2012; Correa-Lima et al. 2019; Remolina-Figueroa et al. 2022; Remolina-Figueroa et al. 2022; Sonne et al. 2022; Remolina-Figueroa et al. 2026), drought (Smith 1982; Stiles 1992; Arroyo et al. 2020), or land-use change (Tinoco et al. 2017; Hadley et al. 2018; Prieto-Torres et al. 2021; Guevara et al. 2023). Now more than ever, it is critical to understand how hummingbirds will respond to environmental disturbances so that we might develop conservation strategies tailored to these tiny pollinators (English et al. 2022).

Our work here can be distilled to five overarching takeaways: **(1)** A bird’s share of feeder time at the beginning of the experiment remained a stable trait as the study progressed, predicting several other “downstream” results; ultimately, the access hierarchy was robust to resource manipulation. **(2)** The costs of scarcity and corresponding competition were largely borne by low-access birds—which disproportionately dropped out of the feeder system—and some species that were more vulnerable, possibly due to different life-history traits. **(3)** Birds did not temporally partition to quieter times of day to reduce competition, but rather compressed their activity spans even more, especially low-access birds. **(4)** Foraging strategies across the assemblage formed a continuum, with birds retaining their own idiosyncratic signatures while modifying their strategies under scarcity. **(5)** Recovery from the manipulation was partial and slow, with many components of behavior (throughput, dropout, turnover, visit durations, top-feeder shares, and visit frequencies) failing to rebound completely once we had reinstated all the feeders. In summary, it appears that hummingbird assemblages reliant on feeders might buffer against rapid resource loss through hierarchical filtering, which structures which birds remain, and how the assemblage has reorganized, once the disturbance has come to an end.

Declarations

Ethics approval and consent to participate

We conducted all work under the approval of the University of Washington's Institutional Animal Care and Use Committee (IACUC protocol number: 4498-05), and our research permit was issued by Instituto Alexander von Humboldt (permit number: 22-225).

Competing interests

The authors declare that they have no competing interests.

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Authors' contributions

Lead author AJS led the investigation, project design, project administration, validation, visualization, statistical analysis, figure/table preparation, and writing all drafts of the manuscript; senior author ARG led supervision efforts, and co-led project conceptualization and funding acquisition efforts alongside AJS. YW and KF designed the bespoke RFID units used in this experiment. JCR and NM assisted with data cleanup and preparation, while JJF helped guide analytical decision-making. All fieldwork was conducted by AJS and MCF.

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Literature cited

- Abrahamczyk S, Kessler M. 2010. Hummingbird diversity, food niche characters, and assemblage composition along a latitudinal precipitation gradient in the Bolivian lowlands. *J Ornithol.* 151(3):615–625. <https://doi.org/10.1007/s10336-010-0496-x>
- 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(2):333–347. <https://doi.org/10.1007/s10336-014-1146-5>
- Alexandre NM et al. 2025. Supplemental Feeding as a Driver of Population Expansion and Morphological Change in Anna’s Hummingbirds. *Global Change Biology.* 31(5):e70237. <https://doi.org/10.1111/gcb.70237>
- Altshuler DL. 2006. Flight Performance and Competitive Displacement of Hummingbirds across Elevational Gradients. *The American Naturalist.* 167(2):216–229. <https://doi.org/10.1086/498622>
- Altshuler DL, Stiles FG, Dudley R. 2004. Of Hummingbirds and Helicopters: Hovering Costs, Competitive Ability, and Foraging Strategies. *The American Naturalist.* 163(1):16–25. <https://doi.org/10.1086/380511>
- Amarasekare P. 2003. Competitive coexistence in spatially structured environments: a synthesis. *Ecology Letters.* 6(12):1109–1122. <https://doi.org/10.1046/j.1461-0248.2003.00530.x>
- Antunes AZ. 2003. Partilha de néctar de *Eucalyptus* spp., territorialidade e hierarquia de dominância em beija-flores (Aves: Trochilidae) no sudeste do Brasil. 11. 1(39–44)
- Aplin LM et al. 2015. Consistent individual differences in the social phenotypes of wild great tits, *Parus major*. *Animal Behaviour.* 108:117–127. <https://doi.org/10.1016/j.anbehav.2015.07.016>
- Araya-Salas M et al. 2018. Spatial memory is as important as weapon and body size for territorial ownership in a lekking hummingbird. *Scientific Reports.* 8(1):2001. <https://doi.org/10.1038/s41598-018-20441-x>
- Arizmendi M del C et al. 2007. Effect of the presence of nectar feeders on the breeding success of *Salvia mexicana* and *Salvia fulgens* in a suburban park near México City. *Biological Conservation.* 136(1):155–158 (Special section: Coastal Sandplains). <https://doi.org/10.1016/j.biocon.2006.11.016>
- Arroyo MTK et al. 2020. Extreme Drought Affects Visitation and Seed Set in a Plant Species in the Central Chilean Andes Heavily Dependent on Hummingbird Pollination. *Plants.* 9(11):1553. <https://doi.org/10.3390/plants9111553>
- Avalos G, Soto A, Alfaro W. 2012. Effect of artificial feeders on pollen loads of the hummingbirds of Cerro de La Muerte, Costa Rica. *Revista de Biología Tropical.* 60(1):65–73
- Bandivadekar RR et al. 2018. Use of RFID technology to characterize feeder visitations and contact network of hummingbirds in urban habitats. *PLOS ONE.* 13(12):e0208057. <https://doi.org/10.1371/journal.pone.0208057>
- Barreto E et al. 2025. Hummingbird flower visitation rates vary with species traits, floral abundance and phenology across bioregions. *Oikos.* 2025(9):e11354. <https://doi.org/10.1002/oik.11354>
- Bates D, Mächler M, Bolker B, Walker S. 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software.* 67:1–48. <https://doi.org/10.18637/jss.v067.i01>
- Bell AM, Hankison SJ, Laskowski KL. 2009. The repeatability of behaviour: a meta-analysis. *Animal Behaviour.* 77(4):771–783. <https://doi.org/10.1016/j.anbehav.2008.12.022>

- Betts MG, Hadley AS, Kress WJ. 2015. Pollinator recognition by a keystone tropical plant. *PNAS*. 112(11):3433–3438. <https://doi.org/10.1073/pnas.1419522112>
- Beuchat CA, Calder WA, Braun EJ. 1990. The Integration of Osmoregulation and Energy Balance in Hummingbirds. *Physiological Zoology*. 63(6):1059–1081. <https://doi.org/10.1086/physzool.63.6.30152633>
- Beuchat CA, Chaplin SB, Morton ML. 1979. Ambient Temperature and the Daily Energetics of Two Species of Hummingbirds, *Calypte anna* and *Selasphorus rufus*. *Physiological Zoology*. 52(3):280–295. <https://doi.org/10.1086/physzool.52.3.30155751>
- Boag PT, Grant PR. 1984. Darwin's Finches (*Geospiza*) On Isla Daphne Major, Galapagos: Breeding and Feeding Ecology in a Climatically Variable Environment. *Ecological Monographs*. 54(4):463–489. <https://doi.org/10.2307/1942596>
- Bolker BM et al. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*. 24(3):127–135. <https://doi.org/10.1016/j.tree.2008.10.008>
- Brereton JE, Fernandez EJ. 2022. Investigating Unused Tools for the Animal Behavioral Diversity Toolkit. *Animals (Basel)*. 12(21):2984. <https://doi.org/10.3390/ani12212984>
- Bribiesca R et al. 2019. Body mass as a supertrait linked to abundance and behavioral dominance in hummingbirds: A phylogenetic approach. *Ecology and Evolution*. 9(4):1623–1637. <https://doi.org/https://doi.org/10.1002/ece3.4785>
- Brockmeyer T, Schaefer HM. 2012. Do nectar feeders in Andean nature reserves affect flower visitation by hummingbirds? *Basic and Applied Ecology*. 13(3):294–300. <https://doi.org/10.1016/j.baae.2012.02.005>
- Brooks M et al. 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal*. [published online ahead of print] <https://digitalcommons.unl.edu/r-journal/675>
- Calder WA. 1975. Daylength and the Hummingbirds' Use of Time. *The Auk*. 92(1):81–97. <https://doi.org/10.2307/4084419>
- Camfield AF. 2006. Resource value affects territorial defense by Broad-tailed and Rufous hummingbirds. *J Field Ornithology*. 77(2):120–125. <https://doi.org/10.1111/j.1557-9263.2006.00031.x>
- Carpenter FL. 1987. Food Abundance and Territoriality: To Defend or Not to Defend? *Am Zool*. 27(2):387–399. <https://doi.org/10.1093/icb/27.2.387>
- Carpenter FL et al. 1993. Exploitative Compensation by Subordinate Age-Sex Classes of Migrant Rufous Hummingbirds. *Behavioral Ecology and Sociobiology*. 33(5):305–312
- Carpenter FL, Hixon MA, Hunt A, Russell RW. 1991. Why hummingbirds have such large crops. *Evol Ecol*. 5(4):405–414. <https://doi.org/10.1007/BF02214157>
- Carscadden KA et al. 2020. Niche Breadth: Causes and Consequences for Ecology, Evolution, and Conservation. *The Quarterly Review of Biology*. 95(3):179–214. <https://doi.org/10.1086/710388>
- Castro-Arellano I, Lacher Jr TE, Willig MR, Rangel TF. 2010. Assessment of assemblage-wide temporal niche segregation using null models. *Methods in Ecology and Evolution*. 1(3):311–318. <https://doi.org/10.1111/j.2041-210X.2010.00031.x>
- Chesson P. 1991. A need for niches? *Trends in Ecology & Evolution*. 6(1):26–28. [https://doi.org/10.1016/0169-5347\(91\)90144-M](https://doi.org/10.1016/0169-5347(91)90144-M)

- Chesson P. 2000. Mechanisms of Maintenance of Species Diversity. *Annual Review of Ecology, Evolution, and Systematics*. 31(Volume 31, 2000):343–366.
<https://doi.org/10.1146/annurev.ecolsys.31.1.343>
- Chin DD, Lentink D. 2016. Flapping wing aerodynamics: from insects to vertebrates. *Journal of Experimental Biology*. 219(7):920–932. <https://doi.org/10.1242/jeb.042317>
- Chung NC, Miasojedow B, Startek M, Gambin A. 2019. Jaccard/Tanimoto similarity test and estimation methods for biological presence-absence data. *BMC Bioinformatics*. 20(Suppl 15):644. <https://doi.org/10.1186/s12859-019-3118-5>
- Clavel J, Julliard R, Devictor V. 2011. Worldwide decline of specialist species: toward a global functional homogenization? *Frontiers in Ecology and the Environment*. 9(4):222–228.
<https://doi.org/10.1890/080216>
- Cole EF, Quinn JL. 2011. Personality and problem-solving performance explain competitive ability in the wild. *Proc Biol Sci*. 279(1731):1168–1175.
<https://doi.org/10.1098/rspb.2011.1539>
- Colles A, Liow LH, Prinzing A. 2009. Are specialists at risk under environmental change? Neoecological, paleoecological and phylogenetic approaches. *Ecology Letters*. 12(8):849–863. <https://doi.org/10.1111/j.1461-0248.2009.01336.x>
- Correa-Lima APA, Varassin IG, Barve N, Zwiener VP. 2019. Spatio-temporal effects of climate change on the geographical distribution and flowering phenology of hummingbird-pollinated plants. *Ann Bot*. 124(3):389–398. <https://doi.org/10.1093/aob/mcz079>
- Cotton PA. 1998. Temporal partitioning of a floral resource by territorial hummingbirds. *Ibis*. 140(4):647–653. <https://doi.org/https://doi.org/10.1111/j.1474-919X.1998.tb04710.x>
- Craig JL, Douglas ME. 1984. Temporal partitioning of a nectar resource in relation to competitive asymmetries. *Animal Behaviour*. 32(2):624–625. [https://doi.org/10.1016/S0003-3472\(84\)80300-0](https://doi.org/10.1016/S0003-3472(84)80300-0)
- Davies ZG et al. 2012. Household Factors Influencing Participation in Bird Feeding Activity: A National Scale Analysis. *PLOS ONE*. 7(6):e39692.
<https://doi.org/10.1371/journal.pone.0039692>
- Dearborn DC. 1998. Interspecific Territoriality by a Rufous-Tailed Hummingbird (*Amazilia tzacatl*): Effects of Intruder Size and Resource Value. *Biotropica*. 30(2):306–313.
<https://doi.org/10.1111/j.1744-7429.1998.tb00064.x>
- Delgado-Martínez CM, Kolb M, Pascual-Ramírez F, Mendoza E. 2023. Differential utilization of surface and arboreal water bodies by birds and mammals in a seasonally dry Neotropical forest in southern Mexico. *Ecol Evol*. 13(11):e10781. <https://doi.org/10.1002/ece3.10781>
- Devictor V, Julliard R, Jiguet F. 2008. Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. *Oikos*. 117(4):507–514.
<https://doi.org/10.1111/j.0030-1299.2008.16215.x>
- Di Cecco GJ, Hurlbert AH. 2022. Multiple dimensions of niche specialization explain changes in species' range area, occupancy, and population size. *Front Ecol Evol*. 10 [accessed 2026 May 14]. <https://www.frontiersin.org/journals/ecology-and-evolution/articles/10.3389/fevo.2022.921480/full>. <https://doi.org/10.3389/fevo.2022.921480>
- Duque FG et al. 2020. High-frequency hearing in a hummingbird. *Science Advances*. 6(29):eabb9393. <https://doi.org/10.1126/sciadv.abb9393>
- Eberts ER, Dick MF, Welch KC. 2019. Metabolic Fates of Evening Crop-Stored Sugar in Ruby-Throated Hummingbirds (*Archilochus colubris*). *Diversity*. 11(1):9.
<https://doi.org/10.3390/d11010009>

- Echevarría G, Buitrón-Jurado G. 2025. Using Smartphones to Determine Hummingbird Dominance Networks in Quinde Ecotourist-Route, Ecuador. *Biotropica*. 57(4):e70061. <https://doi.org/10.1111/btp.70061>
- Elting RL et al. 2026. Foraging plasticity and physiological adaptations enable hummingbirds to subsist on dilute nectars. *Functional Ecology*. 40(5):1475–1490. <https://doi.org/10.1111/1365-2435.70308>
- English SG et al. 2022. Quantifying phenology and migratory behaviours of hummingbirds using single-site dynamics and mark-detection analyses. *Proceedings of the Royal Society B: Biological Sciences*. 289(1982):20220991. <https://doi.org/10.1098/rspb.2022.0991>
- Ewald PW, Carpenter FL. 1978. Territorial Responses to Energy Manipulations in the Anna Hummingbird. *Oecologia*. 31(3):277–292
- Falk JJ, Sargent AJ, Medina J, Rico-Guevara A. 2025. The daily life of a hummingbird: High-throughput tracking shows a spectrum of feeding and movement strategies. 2025.02.25.640146 [accessed 2026 May 14]. <https://www.biorxiv.org/content/10.1101/2025.02.25.640146v1>. <https://doi.org/10.1101/2025.02.25.640146>
- Farine DR, Carter GG. 2022. Permutation tests for hypothesis testing with animal social network data: Problems and potential solutions. *Methods in Ecology and Evolution*. 13(1):144–156. <https://doi.org/10.1111/2041-210X.13741>
- Feinsinger P. 1976. Organization of a Tropical Guild of Nectarivorous Birds. *Ecological Monographs*. 46(3):257–291. <https://doi.org/10.2307/1942255>
- Ferrari S, Cribari-Neto F. 2004. Beta Regression for Modelling Rates and Proportions. *Journal of Applied Statistics*. 31(7):799–815. <https://doi.org/10.1080/0266476042000214501>
- Ferry N, Dray S, Fritz H, Valeix M. 2016. Interspecific interference competition at the resource patch scale: do large herbivores spatially avoid elephants while accessing water? *J Anim Ecol*. 85:1574–1585
- Foley JA et al. 2005. Global Consequences of Land Use. *Science*. 309(5734):570–574. <https://doi.org/10.1126/science.1111772>
- Francis ML et al. 2018. Effects of supplementary feeding on interspecific dominance hierarchies in garden birds. *PLOS ONE*. 13(9):e0202152. <https://doi.org/10.1371/journal.pone.0202152>
- Friedl H, Stampfer E. 2006. Jackknife Resampling. In: *Encyclopedia of Environmetrics*. John Wiley & Sons, Ltd [accessed 2026 May 11]. <https://onlinelibrary.wiley.com/doi/abs/10.1002/9780470057339.vaj001>. <https://doi.org/10.1002/9780470057339.vaj001>
- Galbraith JA et al. 2017. Urban Bird Feeders Dominated by a Few Species and Individuals. *Frontiers in Ecology and Evolution*. 5 <https://www.frontiersin.org/articles/10.3389/fevo.2017.00081>
- Garrison JSE, Gass CL. 1999. Response of a traplining hummingbird to changes in nectar availability. *Behav Ecol*. 10(6):714–725. <https://doi.org/10.1093/beheco/10.6.714>
- Gass CL, Romich MT, Suarez RK. 1999. Energetics of hummingbird foraging at low ambient temperature. *Can J Zool*. 77(2):314–320. <https://doi.org/10.1139/z98-221>
- Gelardi V, Fagot J, Barrat A, Claidière N. 2019. Detecting social (in)stability in primates from their temporal co-presence network. *Animal Behaviour*. 157:239–254. <https://doi.org/10.1016/j.anbehav.2019.09.011>

- Gilbert NA, Stenglein JL, Pauli JN, Zuckerberg B. 2022. Human disturbance compresses the spatiotemporal niche. *Proceedings of the National Academy of Sciences*. 119(52):e2206339119. <https://doi.org/10.1073/pnas.2206339119>
- Gill FB, Wolf LL. 1975. Economics of Feeding Territoriality in the Golden-Winged Sunbird. *Ecology*. 56(2):333–345. <https://doi.org/10.2307/1934964>
- Goertz J, Morris A, Morris S. 1980. Ruby-throated Hummingbirds Feed at Night with the Aid of Artificial Light. *Wilson Bulletin*. 92(3) https://digitalcommons.usf.edu/wilson_bulletin/vol92/iss3/15
- Gowda V, Temeles EJ, Kress WJ. 2012. Territorial Fidelity to Nectar Sources by Purple-throated Caribs, *Eulampis Jugularis*. *The Wilson Journal of Ornithology*. 124(1):81–86. <https://doi.org/10.1676/11-061.1>
- Grant JWA. 1993. Whether or not to defend? The influence of resource distribution. *Marine & Freshwater Behaviour & Phy*. 23(Issue 1-4: Behavioural Ecology of Fishes):137–153. <https://doi.org/https://doi.org/10.1080/10236249309378862>
- Greig EI, Wood EM, Bonter DN. 2017. Winter range expansion of a hummingbird is associated with urbanization and supplementary feeding. *Proceedings of the Royal Society B: Biological Sciences*. 284(1852):20170256. <https://doi.org/10.1098/rspb.2017.0256>
- Guevara EA et al. 2023. Hummingbird community structure and nectar resources modulate the response of interspecific competition to forest conversion. *Oecologia*. 201(3):761–770. <https://doi.org/10.1007/s00442-023-05330-z>
- Gwet KL. 2014. *Handbook of Inter-Rater Reliability, 4th Edition: The Definitive Guide to Measuring The Extent of Agreement Among Raters*. Advanced Analytics, LLC.
- Hadley AS, Betts MG. 2009. Tropical deforestation alters hummingbird movement patterns. *Biol Lett*. 5(2):207–210. <https://doi.org/10.1098/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(1):74–83. <https://doi.org/https://doi.org/10.1111/btp.12487>
- Hainsworth FR, Tardiff MF, Wolf LL. 1981. Proportional Control for Daily Energy Regulation in Hummingbirds. *Physiological Zoology*. 54(4):452–462
- Hair Jr JF, Black WC, Babin BJ, Anderson RE. 2010. Multivariate data analysis. In: *Multivariate data analysis*. p 785–785 [accessed 2026 May 11]. <https://pesquisa.bvsalud.org/portal/resource/pt/biblio-1074274>
- Halter SR. 2026. *Energy Management and Water Balance in Migrating Hummingbirds* [Ph.D.]. The University of New Mexico. [accessed 2026 July 21]. <https://www.proquest.com/docview/3353145876/abstract/5D749EF099246BDPQ/1>
- Harrison ND, Kelly EL. 2022. Affordable RFID loggers for monitoring animal movement, activity, and behaviour. *PLOS ONE*. 17(10):e0276388. <https://doi.org/10.1371/journal.pone.0276388>
- Hartig F, Lohse L, leite M de S. 2024. DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. [accessed 2025 Jan 28]. <https://cran.r-project.org/web/packages/DHARMA/index.html>
- Hastings A. 2001. Transient dynamics and persistence of ecological systems. *Ecology Letters*. 4(3):215–220. <https://doi.org/10.1046/j.1461-0248.2001.00220.x>
- Hazlehurst JA, Karubian JO. 2018. Impacts of nectar robbing on the foraging ecology of a territorial hummingbird. *Behavioural Processes*. 149:27–34. <https://doi.org/10.1016/j.beproc.2018.01.001>

- Healy SD, Hurly TA. 2013. What hummingbirds can tell us about cognition in the wild. CCB. 8:13–28. <https://doi.org/10.3819/ccbr.2013.80002>
- Hiebert SM. 1991. Seasonal Differences in the Response of Rufous Hummingbirds to Food Restriction: Body Mass and the Use of Torpor. *The Condor: Ornithological Applications*. 93(3):526–537. <https://doi.org/10.2307/1368184>
- 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(3):366–391
- Hopkins B, Skellam JG. 1954. A New Method for determining the Type of Distribution of Plant Individuals. *Ann Bot*. 18(2):213–227. <https://doi.org/10.1093/oxfordjournals.aob.a083391>
- Hughes EJ, Mady RP, Bonter DN. 2021. Evaluating the accuracy and biological meaning of visits to RFID-enabled bird feeders using video. *Ecology and Evolution*. 11(23):17132–17141. <https://doi.org/10.1002/ece3.8352>
- Hurly AT. 2003. The twin threshold model: risk-intermediate foraging by rufous hummingbirds, *Selasphorus rufus*. *Animal Behaviour*. 66(4):751–761. <https://doi.org/10.1006/anbe.2003.2278>
- Jones DN, Reynolds SJ. 2008. Feeding birds in our towns and cities: a global research opportunity. *Journal of Avian Biology*. 39(3):265–271. <https://doi.org/10.1111/j.0908-8857.2008.04271.x>
- Justino DG, Maruyama PK, Oliveira PE. 2012. Floral resource availability and hummingbird territorial behaviour on a Neotropical savanna shrub. *J Ornithol*. 153(1):189–197. <https://doi.org/10.1007/s10336-011-0726-x>
- Kaiser HF. 1960. The Application of Electronic Computers to Factor Analysis. *Educational and Psychological Measurement*. 20(1):141–151. <https://doi.org/10.1177/001316446002000116>
- Karakoç C et al. 2017. Transient recovery dynamics of a predator–prey system under press and pulse disturbances. *BMC Ecol*. 17(1):13. <https://doi.org/10.1186/s12898-017-0123-2>
- Keddy PA. 2001. Studying competition. In: Keddy PA, editor. *Competition*. Springer Netherlands; p 1–59 [accessed 2026 July 3]. https://doi.org/10.1007/978-94-010-0694-1_1
- Kneitel J. 2008. Gause's Competitive Exclusion Principle. In: Jørgensen SE, Fath BD, editors. *Encyclopedia of Ecology*. Academic Press; p 1731–1734 [accessed 2026 July 25]. <https://www.sciencedirect.com/science/article/pii/B9780080454054007941>. <https://doi.org/10.1016/B978-008045405-4.00794-1>
- Kodric-Brown A, Brown JH. 1978. Influence of Economics, Interspecific Competition, and Sexual Dimorphism on Territoriality of Migrant Rufous Hummingbirds. *Ecology*. 59(2):285–296. <https://doi.org/https://doi.org/10.2307/1936374>
- Krebs JR, Harvey PH. 1986. Avian physiology: Busy doing nothing—efficiently. *Nature*. 320(6057):18–19. <https://doi.org/10.1038/320018a0>
- Kronfeld-Schor N, Dayan T. 2003. Partitioning of Time as an Ecological Resource. *Annual Review of Ecology, Evolution, and Systematics*. 34(Volume 34, 2003):153–181. <https://doi.org/10.1146/annurev.ecolsys.34.011802.132435>
- Lanna LL et al. 2017. Feeding behavior by hummingbirds (Aves: Trochilidae) in artificial food patches in an Atlantic Forest remnant in southeastern Brazil. *Zoologia (Curitiba)*. 34 [accessed 2021 Feb 4]. http://www.scielo.br/scielo.php?script=sci_abstract&pid=S1984-46702017000100305&lng=en&nrm=iso&tlng=en. <https://doi.org/10.3897/zoologia.34.e13228>

- Lara C et al. 2011. Temporal-spatial segregation among hummingbirds foraging on honeydew in a temperate forest in Mexico. *Curr Zool.* 57(1):56–62. <https://doi.org/10.1093/czoolo/57.1.56>
- Lara C, Lumbreras K, González M. 2009. Niche partitioning among hummingbirds foraging on *Penstemon roseus* (Plantaginaceae) in central Mexico. *Neotrop Ornithol.* 20
- Lawson B et al. 2018. Health hazards to wild birds and risk factors associated with anthropogenic food provisioning. *Philos Trans R Soc Lond B Biol Sci.* 373(1745):20170091. <https://doi.org/10.1098/rstb.2017.0091>
- Lenth RV. 2021. emmeans: Estimated Marginal Means, aka Least-Squares Means. <https://cran.r-project.org/package=emmeans>
- Lewis SL, Maslin MA. 2015. Defining the Anthropocene. *Nature.* 519(7542):171–180. <https://doi.org/10.1038/nature14258>
- Lindberg AB, Olesen JM. 2001. The fragility of extreme specialization: *Passiflora mixta* and its pollinating hummingbird *Ensifera ensifera*. *Journal of Tropical Ecology.* 17(2):323–329. <https://doi.org/10.1017/S0266467401001213>
- Lindsay JM et al. 2026. Ringed Seal (*Pusa hispida*) Haul-Out Behavior and Emergence Timing in the Bering, Chukchi, and Beaufort Seas. *Ecology and Evolution.* 16(1):e72948. <https://doi.org/10.1002/ece3.72948>
- Łomnicki A. 2009. Scramble and contest competition, unequal resource allocation, and resource monopolization as determinants of population dynamics. *Evolutionary Ecology Research.* 11
- López-Calleja MV, Bozinovic F, Martinez del Rio C. 1997. Effects of sugar concentration on hummingbird feeding and energy use. *Comparative Biochemistry and Physiology Part A: Physiology.* 118(4):1291–1299. [https://doi.org/10.1016/S0300-9629\(97\)00243-0](https://doi.org/10.1016/S0300-9629(97)00243-0)
- López-Segoviano G, Arenas-Navarro M, Vega E, Arizmendi M del C. 2018. Hummingbird migration and flowering synchrony in the temperate forests of northwestern Mexico. *PeerJ.* 6:e5131. <https://doi.org/10.7717/peerj.5131>
- Lyon DL. 1976. A Montane Hummingbird Territorial System in Oaxaca, Mexico. *The Wilson Bulletin.* 88(2):280–299
- Mady RP, Hochachka WM, Bonter DN. 2021. Consistency in supplemental food availability affects the space use of wintering birds. *Behav Ecol.* 32(4):580–589. <https://doi.org/10.1093/beheco/arab002>
- Maglianesi MA, Blüthgen N, Böhning-Gaese K, Schleuning M. 2015. Functional structure and specialization in three tropical plant–hummingbird interaction networks across an elevational gradient in Costa Rica. *Ecography.* 38(11):1119–1128. <https://doi.org/10.1111/ecog.01538>
- Maglianesi MA, Böhning-Gaese K, Schleuning M. 2015. Different foraging preferences of hummingbirds on artificial and natural flowers reveal mechanisms structuring plant–pollinator interactions. *J Anim Ecol.* 84(3):655–664. <https://doi.org/10.1111/1365-2656.12319>
- Magnhagen C et al. 2014. Context Consistency and Seasonal Variation in Boldness of Male Two-Spotted Gobies. *PloS one.* 9:e93354. <https://doi.org/10.1371/journal.pone.0093354>
- Mailly J, Riotte-Lambert L, Lihoreau M. 2025. How pollinator movement patterns emerge from the interaction between cognition and the environment. *Proceedings of the Royal Society B: Biological Sciences.* 292(2044):20242271. <https://doi.org/10.1098/rspb.2024.2271>
- Manikowska-Ślepowrońska B, Ślepowroński K. 2025. Is Winter Feeder Visitation by Songbirds Risk-Dependent? An Experimental Study. *Birds.* 6(3):45. <https://doi.org/10.3390/birds6030045>

- Márquez-Luna U, Arizmendi M del C. 2025. Importance of feeders in the seasonal dynamics of floral resource use by hummingbirds in Mexico City. *Urban Ecosyst.* 28(2):13. <https://doi.org/10.1007/s11252-024-01664-5>
- Márquez-Luna U, Lara C, Corcuera P, Valverde PL. 2019. Factors affecting the dominance hierarchy dynamics in a hummingbird assemblage. *Current Zoology.* 65(3):261–268. <https://doi.org/10.1093/cz/zoy057>
- Maziarz M et al. 2023. Temporal avoidance as a means of reducing competition between sympatric species. *R Soc Open Sci.* 10(5):230521. <https://doi.org/10.1098/rsos.230521>
- McCaffrey RE, Wethington SM. 2008. How the Presence of Feeders Affects the Use of Local Floral Resources by Hummingbirds: A Case Study from Southern Arizona. *The Condor: Ornithological Applications.* 110(4):786–791. <https://doi.org/10.1525/cond.2008.8621>
- McKinney AM et al. 2012. Asynchronous changes in phenology of migrating Broad-tailed Hummingbirds and their early-season nectar resources. *Ecology.* 93(9):1987–1993. <https://doi.org/10.1890/12-0255.1>
- McWhorter TJ, Martínez del Rio C. 1999. Food ingestion and water turnover in hummingbirds: how much dietary water is absorbed? *J Exp Biol.* 202(20):2851–2858. <https://doi.org/10.1242/jeb.202.20.2851>
- Meehan TD et al. 2020. Interacting with hummingbirds at home: Associations with supplemental feeding, plant diversity, plant origin, and landscape setting. *Landscape and Urban Planning.* 197:103774. <https://doi.org/10.1016/j.landurbplan.2020.103774>
- Mendonça LB, Anjos L dos. 2005. Hummingbirds (Aves, Trochilidae) and their flowers in an urban area of southern Brazil. *Rev Bras Zool.* 22:51–59. <https://doi.org/https://doi.org/10.1590/S0101-81752005000100007>
- Miller ET et al. 2017. Fighting over food unites the birds of North America in a continental dominance hierarchy. *Behav Ecol.* 28(6):1454–1463. <https://doi.org/10.1093/beheco/axx108>
- Milles A et al. 2023. Local buffer mechanisms for population persistence. *Trends in Ecology & Evolution.* 38(11):1051–1059. <https://doi.org/10.1016/j.tree.2023.06.006>
- Montgomerie RD, Redsell CA. 1980. A Nesting Hummingbird Feeding Solely on Arthropods. *The Condor.* 82(4):463. <https://doi.org/10.2307/1367577>
- Nelson AS, Mooney KA. 2025. Different Aspects of Dominance Are Not Equivalent When Testing for Trade-Offs in Ant Communities. *Ecol Evol.* 15(9):e72207. <https://doi.org/10.1002/ece3.72207>
- Nemiroff L, Despland E. 2007. Consistent individual differences in the foraging behaviour of forest tent caterpillars (*Malacosoma disstria*). *Can J Zool.* 85(11):1117–1124. <https://doi.org/10.1139/Z07-081>
- Parmesan C, Yohe G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature.* 421(6918):37–42. <https://doi.org/10.1038/nature01286>
- Pearson OP. 1954. The Daily Energy Requirements of a Wild Anna Hummingbird. *The Condor.* 56(6):317–322. <https://doi.org/10.2307/1365017>
- Phillips RA, Xavier JC, Croxall JP. 2003. Effects of Satellite Transmitters on Albatrosses and Petrels. *The Auk.* 120(4):1082–1090. <https://doi.org/10.1093/auk/120.4.1082>
- Pimm SL. 1978. An Experimental Approach to the Effects of Predictability on Community Structure. *Am Zool.* 18(4):797–808. <https://doi.org/10.1093/icb/18.4.797>
- Pimm SL, Rosenzweig ML, Mitchell W. 1985. Competition and Food Selection: Field Tests of a Theory. *Ecology.* 66(3):798–807. <https://doi.org/https://doi.org/10.2307/1940541>

- Portugal SJ, White CR. 2018. Miniaturization of biologgers is not alleviating the 5% rule. *Methods in Ecology and Evolution*. 9(7):1662–1666. <https://doi.org/10.1111/2041-210X.13013>
- 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(3):389–397. <https://doi.org/10.1086/374286>
- Powers DR, Conley TM. 1994. Field Metabolic Rate and Food Consumption of Two Sympatric Hummingbird Species in Southeastern Arizona. *The Condor: Ornithological Applications*. 96(1):141–150. <https://doi.org/10.2307/1369071>
- Powers DR, McKee T. 1994. The Effect of Food Availability on Time and Energy Expenditures of Territorial and Non-Territorial Hummingbirds. *The Condor*. 96(4):1064–1075. <https://doi.org/10.2307/1369115>
- Powers DR, Nagy KA. 1988. Field Metabolic Rate and Food Consumption by Free-Living Anna's Hummingbirds (*Calypte anna*). *Physiological Zoology*. 61(6):500–506. <https://doi.org/10.1086/physzool.61.6.30156158>
- Prieto-Torres DA, Nuñez Rosas LE, Remolina Figueroa D, Arizmendi M del C. 2021. Most Mexican hummingbirds lose under climate and land-use change: Long-term conservation implications. *Perspectives in Ecology and Conservation*. 19(4):487–499. <https://doi.org/10.1016/j.pecon.2021.07.001>
- R Core Team. 2022. R: A language and environment for statistical computing. <https://www.R-project.org/>
- Ramírez-Burbano MB et al. 2022. Nectar provision attracts hummingbirds and connects interaction networks across habitats. *Ibis*. 164(1):88–101. <https://doi.org/10.1111/ibi.12988>
- Ratto F et al. 2018. Global importance of vertebrate pollinators for plant reproductive success: a meta-analysis. *Frontiers in Ecology and the Environment*. 16(2):82–90. <https://doi.org/10.1002/fee.1763>
- Remolina-Figueroa D et al. 2022. Together forever? Hummingbird-plant relationships in the face of climate warming. *Climatic Change*. 175(1):2. <https://doi.org/10.1007/s10584-022-03447-3>
- Remolina-Figueroa D et al. 2026. Relevance of ecological and phylogenetic structure of hummingbird-plant relationships in the face of global climate change. *Perspectives in Ecology and Conservation*. 24(2):191–198. <https://doi.org/10.1016/j.pecon.2026.02.004>
- Rico-Guevara A, Hurme KJ, Elting R, Russell AL. 2021. Bene‘fit’ assessment in pollination coevolution: mechanistic perspectives on hummingbird bill-flower matching. *Integrative and Comparative Biology*. [published online ahead of print] [accessed 2021 July 15]. <https://doi.org/10.1093/icb/icab111>. <https://doi.org/10.1093/icb/icab111>
- Robb GN, McDonald RA, Chamberlain DE, Bearhop S. 2008. Food for thought: supplementary feeding as a driver of ecological change in avian populations. *Frontiers in Ecol & Environ*. 6(9):476–484. <https://doi.org/10.1890/060152>
- Rodríguez-Flores CI, Arizmendi Arriaga MC. 2016. The dynamics of hummingbird dominance and foraging strategies during the winter season in a highland community in Western Mexico. *Journal of Zoology*. 299(4):262–274. <https://doi.org/10.1111/jzo.12360>
- Rojas BG, Espinosa CI, Graham CH, Tinoco BA. 2026. Hummingbird interaction niche packing is influenced by species richness and resource availability in the southern tropical Andes. *Functional Ecology*. 40(7):2275–2285. <https://doi.org/10.1111/1365-2435.70321>
- Rotics S, Clutton-Brock T. 2021. Group size increases inequality in cooperative behaviour. *Proc Biol Sci*. 288(1945):20202104. <https://doi.org/10.1098/rspb.2020.2104>

- Rousseeuw PJ. 1987. Silhouettes: A graphical aid to the interpretation and validation of cluster analysis. *Journal of Computational and Applied Mathematics*. 20:53–65.
[https://doi.org/10.1016/0377-0427\(87\)90125-7](https://doi.org/10.1016/0377-0427(87)90125-7)
- Rousseu F, Charette Y, Bélisle M. 2014. Resource defense and monopolization in a marked population of ruby-throated hummingbirds (*Archilochus colubris*). *Ecology and Evolution*. 4(6):776–793. <https://doi.org/10.1002/ece3.972>
- Rueda-Urbe C et al. 2026. Movement Strategies of Neotropical Nectarivorous Birds: Insights From High-Andean Hummingbirds and Flowerpiercers. *Biotropica*. 58(1):e70132.
<https://doi.org/10.1111/btp.70132>
- Sandlin EA. 2000. Foraging information affects the nature of competitive interactions. *Oikos*. 91(1):18–28. <https://doi.org/10.1034/j.1600-0706.2000.910102.x>
- Sargent AJ et al. 2026. Variable evidence of radio-tag backpacks affecting hummingbird time budgets in captivity. *Anim Biotelemetry*. 14(1):11. <https://doi.org/10.1186/s40317-026-00446-4>
- Sargent AJ, Groom DJE, Rico-Guevara A. 2021. Locomotion and Energetics of Divergent Foraging Strategies in Hummingbirds: A Review. *Integrative and Comparative Biology*. 61(2):736–748. <https://doi.org/10.1093/icb/icab124>
- Schoener TW. 1974. Resource Partitioning in Ecological Communities. *Science*. 185(4145):27–39. <https://doi.org/10.1126/science.185.4145.27>
- Shankar A et al. 2019. Hummingbirds budget energy flexibly in response to changing resources. *Functional Ecology*. 33(10):1904–1916. <https://doi.org/https://doi.org/10.1111/1365-2435.13404>
- Shankar A et al. 2020. Hummingbird torpor in context: duration, more than temperature, is the key to nighttime energy savings. *Journal of Avian Biology*. 51(5) [accessed 2022 Nov 3].
<https://onlinelibrary.wiley.com/doi/abs/10.1111/jav.02305>. <https://doi.org/10.1111/jav.02305>
- Shannon CE. 1948. A mathematical theory of communication. *The Bell System Technical Journal*. 27(3):379–423. <https://doi.org/10.1002/j.1538-7305.1948.tb01338.x>
- Smetzer JR, Paxton KL, Paxton EH. 2021. Individual and seasonal variation in the movement behavior of two tropical nectarivorous birds. *Mov Ecol*. 9(1):36.
<https://doi.org/10.1186/s40462-021-00275-5>
- Smith JM, Parker GA. 1976. The logic of asymmetric contests. *Animal Behaviour*. 24(1):159–175. [https://doi.org/10.1016/S0003-3472\(76\)80110-8](https://doi.org/10.1016/S0003-3472(76)80110-8)
- Smith KG. 1982. Drought-Induced Changes in Avian Community Structure Along a Montane Sere. *Ecology*. 63(4):952–961. <https://doi.org/10.2307/1937235>
- Sonne J et al. 2016. Spatial effects of artificial feeders on hummingbird abundance, floral visitation and pollen deposition. *J Ornithol*. 157(2):573–581. <https://doi.org/10.1007/s10336-015-1287-1>
- Sonne J et al. 2022. Extinction, coextinction and colonization dynamics in plant–hummingbird networks under climate change. *Nat Ecol Evol*. 6(6):720–729.
<https://doi.org/10.1038/s41559-022-01693-3>
- Stevens JP. 2002. *Applied multivariate statistics for the social sciences*, 4th ed. Lawrence Erlbaum Associates Publishers p xiv, 699. (Applied multivariate statistics for the social sciences, 4th ed).
- Stiles FG. 1975. Ecology, Flowering Phenology, and Hummingbird Pollination of Some Costa Rican *Heliconia* Species. *Ecology*. 56(2):285–301.
<https://doi.org/https://doi.org/10.2307/1934961>

- Stiles FG. 1985. Seasonal Patterns and Coevolution in the Hummingbird-Flower Community of a Costa Rican Subtropical Forest. *Ornithological Monographs*. (36):757–787. <https://doi.org/10.2307/40168315>
- Stiles FG. 1992. Effects of a Severe Drought on the Population Biology of a Tropical Hummingbird. *Ecology*. 73(4):1375–1390. <https://doi.org/10.2307/1940683>
- Stiles FG, Wolf LL. 1970. Hummingbird Territoriality at a Tropical Flowering Tree. *The Auk*. 87(3):467–491. <https://doi.org/10.2307/4083791>
- Stiles FG, Wolf LL. 1979. Ecology and Evolution of Lek Mating Behavior in the Long-Tailed Hermit Hummingbird. *Ornithological Monographs*. (27):iii–78. <https://doi.org/10.2307/40166760>
- Stoffel MA, Nakagawa S, Schielzeth H. 2017. rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods in Ecology and Evolution*. 8(11):1639–1644. <https://doi.org/10.1111/2041-210X.12797>
- Stone DB et al. 2019. Intraspecific temporal resource partitioning at white-tailed deer feeding sites. *Curr Zool*. 65(2):139–146. <https://doi.org/10.1093/cz/zoy051>
- Suarez RK et al. 1990. Fuel selection in rufous hummingbirds: ecological implications of metabolic biochemistry. *PNAS*. 87(23):9207–9210. <https://doi.org/10.1073/pnas.87.23.9207>
- Suarez RK. 1992. Hummingbird flight: Sustaining the highest mass-specific metabolic rates among vertebrates. *Experientia*. 48(6):565–570. <https://doi.org/10.1007/BF01920240>
- Suarez RK, Lighton JR, Brown GS, Mathieu-Costello O. 1991. Mitochondrial respiration in hummingbird flight muscles. *Proceedings of the National Academy of Sciences*. 88(11):4870–4873. <https://doi.org/10.1073/pnas.88.11.4870>
- Tellez-Colmenares N, Fernandes AM, Stiles FG, Rico-Guevara A. 2025. Temporal patterns of dominance in a hummingbird assemblage. 2025.12.05.692456 [accessed 2026 May 14]. <https://www.biorxiv.org/content/10.64898/2025.12.05.692456v1>. <https://doi.org/10.64898/2025.12.05.692456>
- Tello-Ramos MC, Hurly AT, Healy SD. 2019. From a sequential pattern, temporal adjustments emerge in hummingbird traplining. *Integrative Zoology*. 14(2):182–192. <https://doi.org/10.1111/1749-4877.12370>
- Tello-Ramos MC, Hurly TA, Healy SD. 2015. Traplining in hummingbirds: flying short-distance sequences among several locations. *Behav Ecol*. 26(3):812–819. <https://doi.org/10.1093/beheco/arv014>
- Tenczar P et al. 2014. Automated monitoring reveals extreme interindividual variation and plasticity in honeybee foraging activity levels. *Animal Behaviour*. 95:41–48. <https://doi.org/10.1016/j.anbehav.2014.06.006>
- Thieurmél B, Elmarhraoui A. 2022. suncalc: Compute Sun Position, Sunlight Phases, Moon Position and Lunar Phase. [accessed 2026 May 14]. <https://cran.r-project.org/web/packages/suncalc/index.html>
- Tiebout HM. 1991. Daytime Energy Management by Tropical Hummingbirds: Responses to Foraging Constraint. *Ecology*. 72(3):839–851. <https://doi.org/10.2307/1940586>
- Tilman D. 1987. The Importance of the Mechanisms of Interspecific Competition. *The American Naturalist*. 129(5):769–774. <https://doi.org/10.1086/284672>
- Tinoco BA, Graham CH, Aguilar JM, Schleuning M. 2017. Effects of hummingbird morphology on specialization in pollination networks vary with resource availability. *Oikos*. 126(1):52–60. <https://doi.org/10.1111/oik.02998>

- Titman D. 1976. Ecological Competition Between Algae: Experimental Confirmation of Resource-Based Competition Theory. *Science*. 192(4238):463–465. <https://doi.org/10.1126/science.192.4238.463>
- Tooze ZJ, Gass CL. 1985. Responses of rufous hummingbirds to midday fasts. *Can J Zool*. 63(10):2249–2253. <https://doi.org/10.1139/z85-333>
- Trigo S, Silva PA, Cardoso GC, Soares MC. 2022. A test of context- and sex-dependent dopaminergic effects on the behavior of a gregarious bird, the common waxbill, *Estrilda astrild*. *J Exp Biol*. 225(6):jeb243861. <https://doi.org/10.1242/jeb.243861>
- Twinomugisha D et al. 2006. How Does the Golden Monkey of the Virungas Cope in a Fruit-Scarce Environment? In: Newton-Fisher NE, Notman H, Paterson JD, Reynolds V, editors. *Primates of Western Uganda*. Springer; p 45–60 [accessed 2026 July 8]. https://doi.org/10.1007/978-0-387-33505-6_3
- Valeix M. 2011. Temporal dynamics of dry-season water-hole use by large African herbivores in two years of contrasting rainfall in Hwange National Park, Zimbabwe. *Journal of Tropical Ecology*. 27(2):163–170. <https://doi.org/10.1017/S0266467410000647>
- Volpe NL, Hadley AS, Robinson WD, Betts MG. 2014. Functional connectivity experiments reflect routine movement behavior of a tropical hummingbird species. *Ecological Applications*. 24(8):2122–2131. <https://doi.org/10.1890/13-2168.1>
- Wagner HO. 1946. Food and Feeding Habits of Mexican Hummingbirds. *The Wilson Bulletin*. 58(2):69–93
- Wallace JW, Diamantides LC, Ki KC, Butler MW. 2020. Switched-Antenna Low-Frequency (LF) Radio-Frequency Identification (RFID) for Ornithology. *IEEE Journal of Radio Frequency Identification*. 4(2):137–145. <https://doi.org/10.1109/JRFID.2020.2971534>
- Walther G-R et al. 2002. Ecological responses to recent climate change. *Nature*. 416(6879):389–395. <https://doi.org/10.1038/416389a>
- Ward-Fear G et al. 2018. The ecological and life history correlates of boldness in free-ranging lizards. *Ecosphere*. 9(3):e02125. <https://doi.org/10.1002/ecs2.2125>
- Weathers WW, Stiles FG. 1989. Energetics and Water Balance in Free-Living Tropical Hummingbirds. *The Condor: Ornithological Applications*. 91(2):324–331. <https://doi.org/10.2307/1368310>
- Weinstein BG, Graham CH. 2016. Evaluating broad scale patterns among related species using resource experiments in tropical hummingbirds. *Ecology*. 97(8):2085–2093. <https://doi.org/10.1890/15-0328.1>
- Wethington SM, Russell SM. 2003. The Seasonal Distribution and Abundance of Hummingbirds in Oak Woodland and Riparian Communities in Southeastern Arizona. *The Condor: Ornithological Applications*. 105(3):484–495. <https://doi.org/10.1093/condor/105.3.484>
- Wilson RP et al. 2002. Remote-sensing systems and seabirds: their use, abuse and potential for measuring marine environmental variables. *Marine Ecology Progress Series*. 228:241–261. <https://doi.org/10.3354/meps228241>
- Zar JH. 2007. *Biostatistical Analysis* (5th Edition). Prentice-Hall, Inc.

Tables

Table 1. Simple experiment-wide descriptive statistics for each access tertile, calculated as across-bird averages of daily individual means. *Total time (s)* represents summed duration of all visits, in seconds; *SD* represents the standard deviation of total time; *visit duration (s)* represents mean visit duration in seconds; *feeders/day* represents the number of units visited; and *activity span (h)* represents hours between the first and last visit made.

Tertile	n birds	Total time (s)	SD	Visits/day	Visit duration (s)	Feeders/day	Activity span (h)
low	37	169	81	11.8	16.8	2.5	3.66
mid	36	429	133	31.5	16.5	3.5	7.54
high	36	850	410	47.6	20.8	3.8	8.50

Table 2. Total feeder time (in seconds) for each access tertile by period, calculated as across-bird averages of daily individual means. Column header parentheses indicate the number of feeders available each period. As captured in Q3 and Q5, every group's visitation time in reinstatement periods fell below their baseline counterparts (A vs. G, B vs. F, and C vs. E), with the exception of low-access birds in period A vs. G (199 s vs. 202 s, respectively).

Tertile	A (16f)	B (12f)	C (8f)	D (4f)	E (8f)	F (12f)	G (16f)
low	199	218	161	123	121	162	202
mid	522	538	441	303	339	410	403
high	1,130	1,107	779	593	624	698	649

Table 3. Number of individuals in each species that ranked as low-, mid-, and high-access, based on per-bird mean total feeder time during period A (the “baseline”). *Chalybura buffonii* clustered strongly in the low tertile (13/18 birds), while *Colibri cyanotus* clustered in the high tertile (8/15). Species are arranged in ascending average body mass.

Species	low	mid	high	Total
<i>Saucerottia cyanifrons</i>	2	5	7	14
<i>Amazilia tzacatl</i>	10	8	6	24
<i>Colibri cyanotus</i>	3	4	8	15
<i>Colibri delphinae</i>	2	2	2	6
<i>Chalybura buffonii</i>	13	2	3	18
<i>Anthracothorax nigricollis</i>	7	15	10	32
Total	37	36	36	109

Table 4. Simple experiment-wide descriptive statistics for each species, calculated as across-bird averages of daily individual means. Species are sorted by ascending average body mass; columns are defined as in Table 1.

Species	n birds	Total time (s)	SD	Visits/day	Visit duration (s)	Feeders/day	Activity span (h)
<i>S. cyanifrons</i>	14	503	309	32.5	18.1	3.1	5.66
<i>Am. tzacatl</i>	24	419	253	25.7	21.0	3.2	5.68
<i>Co. cyanotus</i>	15	642	392	34.8	19.5	3.6	7.17
<i>Co. delphinae</i>	6	545	360	40.7	13.5	2.2	7.75
<i>Ch. buffonii</i>	18	390	634	18.3	20.2	2.8	5.01
<i>An. nigricollis</i>	32	478	274	34.8	14.7	3.6	7.91

Table 5. Species' niche breadths and vulnerabilities to dropout. Estimated marginal means from the best models for each niche axis include activity span from Q5, PC1 scores from Q6, and transition matrix similarity from Q4; model-derived dropout probabilities are from Q2. Species are sorted by descending dropout probability.

Species	Temporal niche (activity span, h)	Feeder selectivity (PC1 score)	Movement regularity (transition matrix similarity)	Model-derived dropout probability
<i>S. cyanifrons</i>	4.14	0.51	0.519	17.98%
<i>Co. cyanotus</i>	6.17	-0.09	0.531	13.22%
<i>Ch. buffonii</i>	6.18	-0.08	0.385	3.76%
<i>Am. tzacatl</i>	5.78	0.05	0.431	3.11%
<i>An. nigricollis</i>	7.33	0.17	0.475	0.84%
<i>Co. delphinae</i>	7.91	1.75	0.636	0.16%

Figures

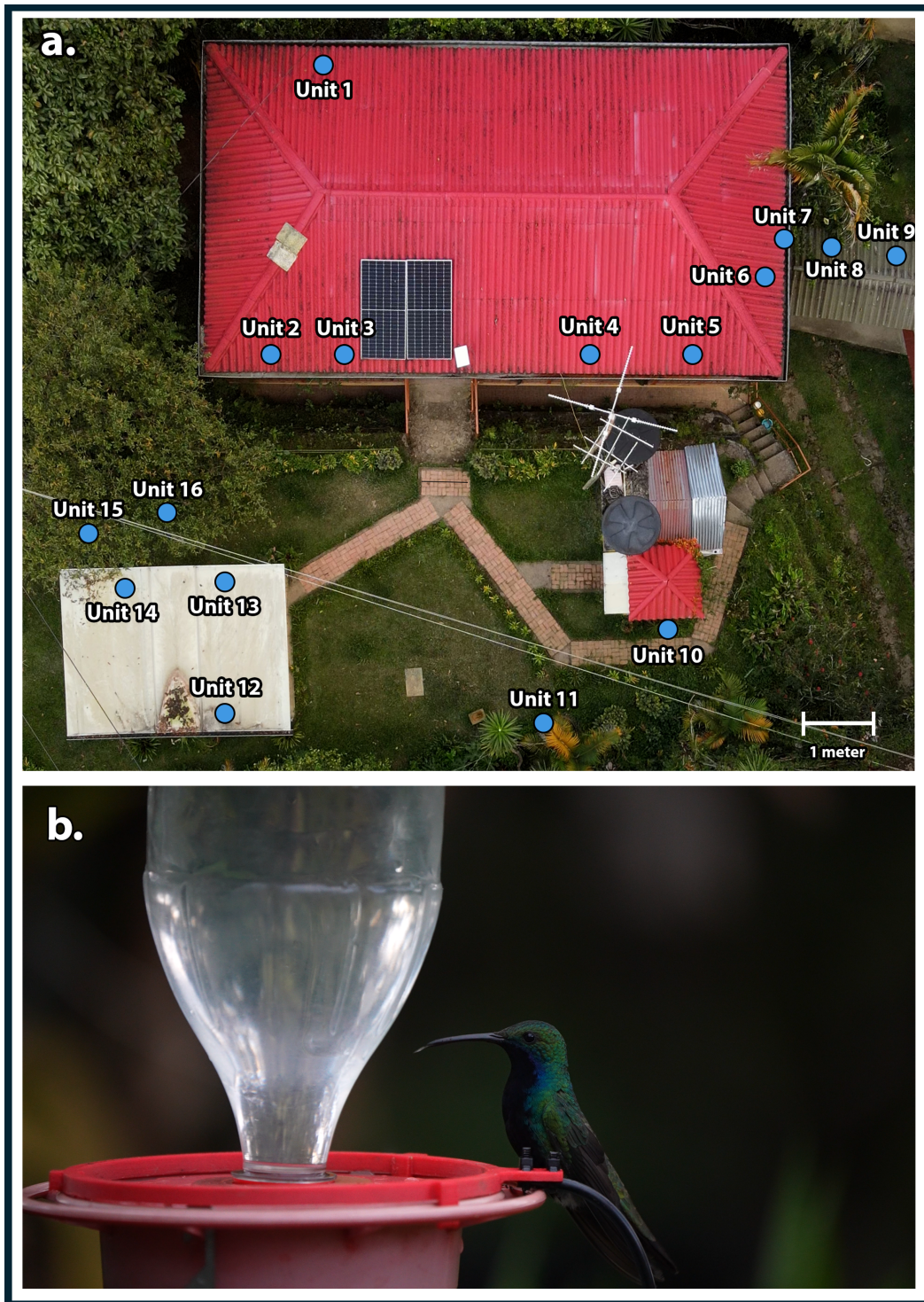


Figure 1. Field site setup. (a) Overhead map of our 16 RFID-enabled feeders (blue points) at Centro de Investigación Colibrí Gorriazul, 12 of which we steadily removed and reinstated throughout the experiment. (b) Custom RFID antenna from units designed at the Humboldt University of Berlin, mounted on one of our feeders (individual in frame is a male *An. nigricollis*). Photographs courtesy of Samantha-Lynn Martinez.

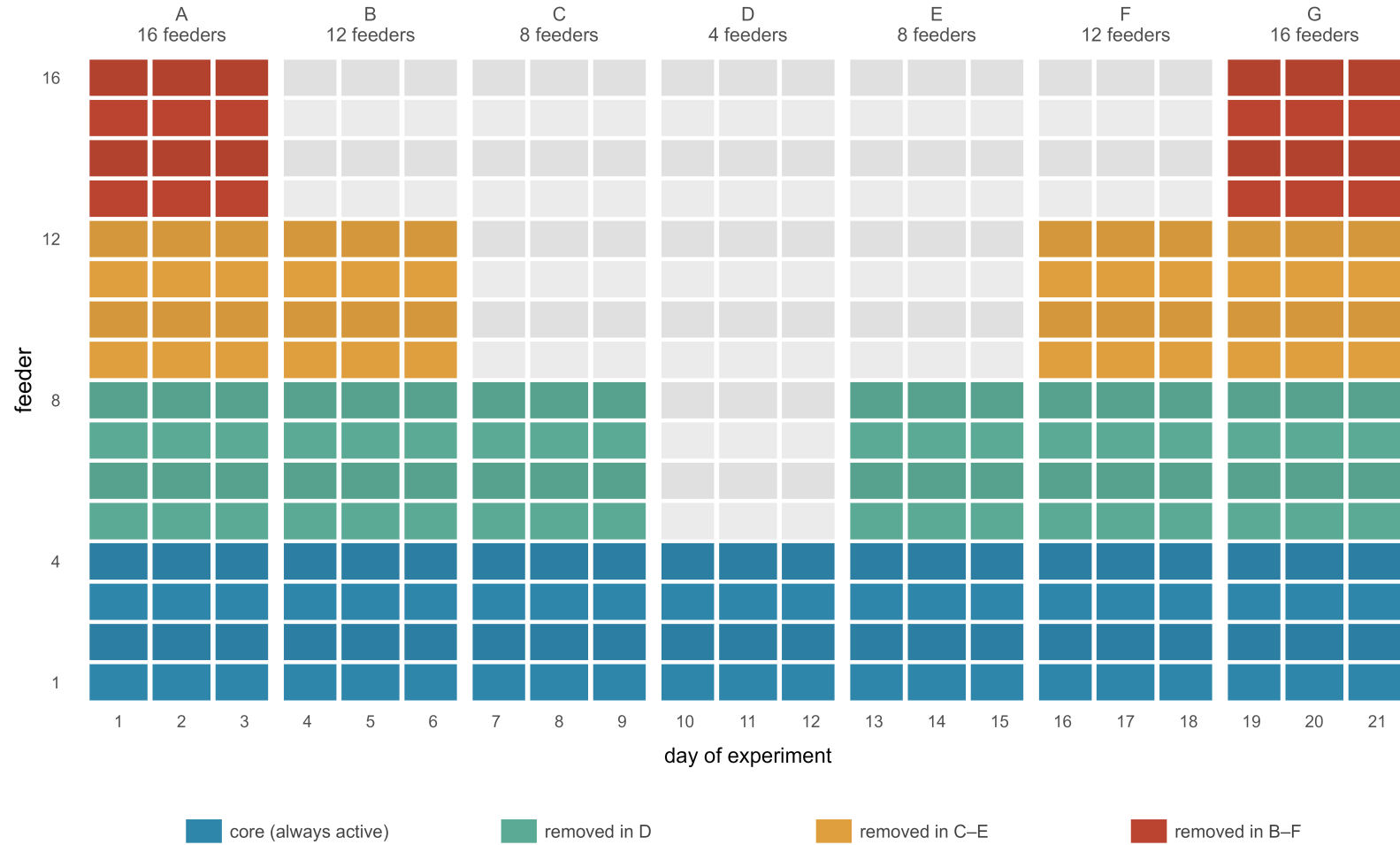


Figure 2. Design of the 21-day feeder manipulation experiment. Each column represents one day, grouped into consecutive three-day periods (represented by letters A–G); each row represents one RFID-enabled feeder. Colors indicate each “group” of feeders, randomly selected for removal (or not) in different periods of the experiment, creating our mirrored removal-and-reinstatement design: Periods A and G had all 16 feeders active (baseline and reinstatement bookends), B and F had 12, C and E had 8, and D had only 4 (peak scarcity). We reinstated the same physical units that we had removed after periods C, B, and A in periods E, F, and G, respectively.

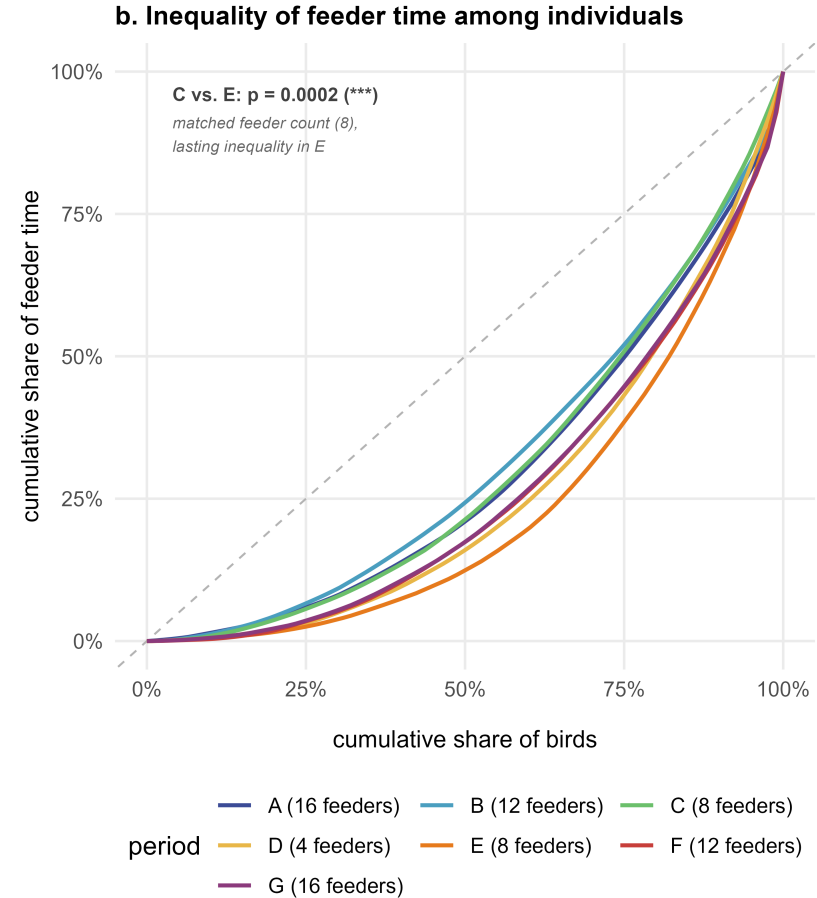
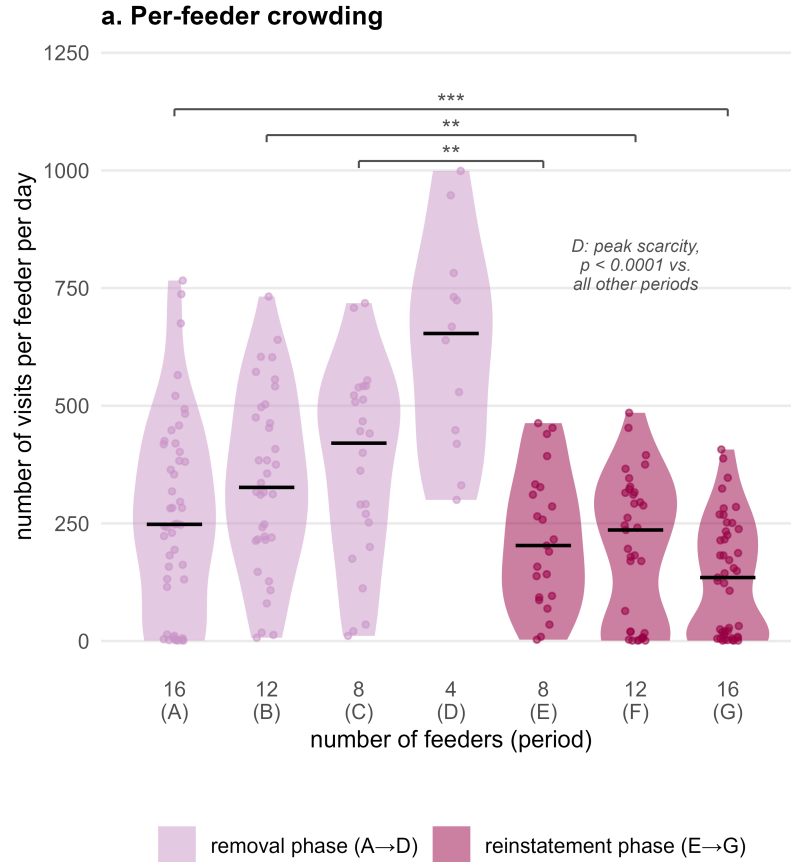


Figure 3. System-level competition across the experiment. (a) Violin plots of daily feeder visit distributions in each period, with points representing the total number of visits received by each feeder on each day ($n = 222$ feeder-days) and black bars representing period medians. Crowding at each feeder peaked in period D, significantly exceeding all other periods ($p < 0.0001$ each, Tukey-corrected), but then fell, with fewer visits to each feeder in the latter half of the experiment (brackets indicate significant mirrored-pair contrasts: ** $p < 0.01$, *** $p < 0.001$); for these statistical tests, we used the site-wide daily mean ($n = 21$ days) of visits to each feeder, adjusted for availability, but we plotted raw values for interpretability. **(b)** Lorenz curves showing the cumulative percentage of birds against the cumulative percentage of feeder time that they had, with the diagonal representing perfect equality, and greater bowing from the diagonal indicating greater inequality. Despite having an identical feeder count, period C had significantly higher inequality than E.

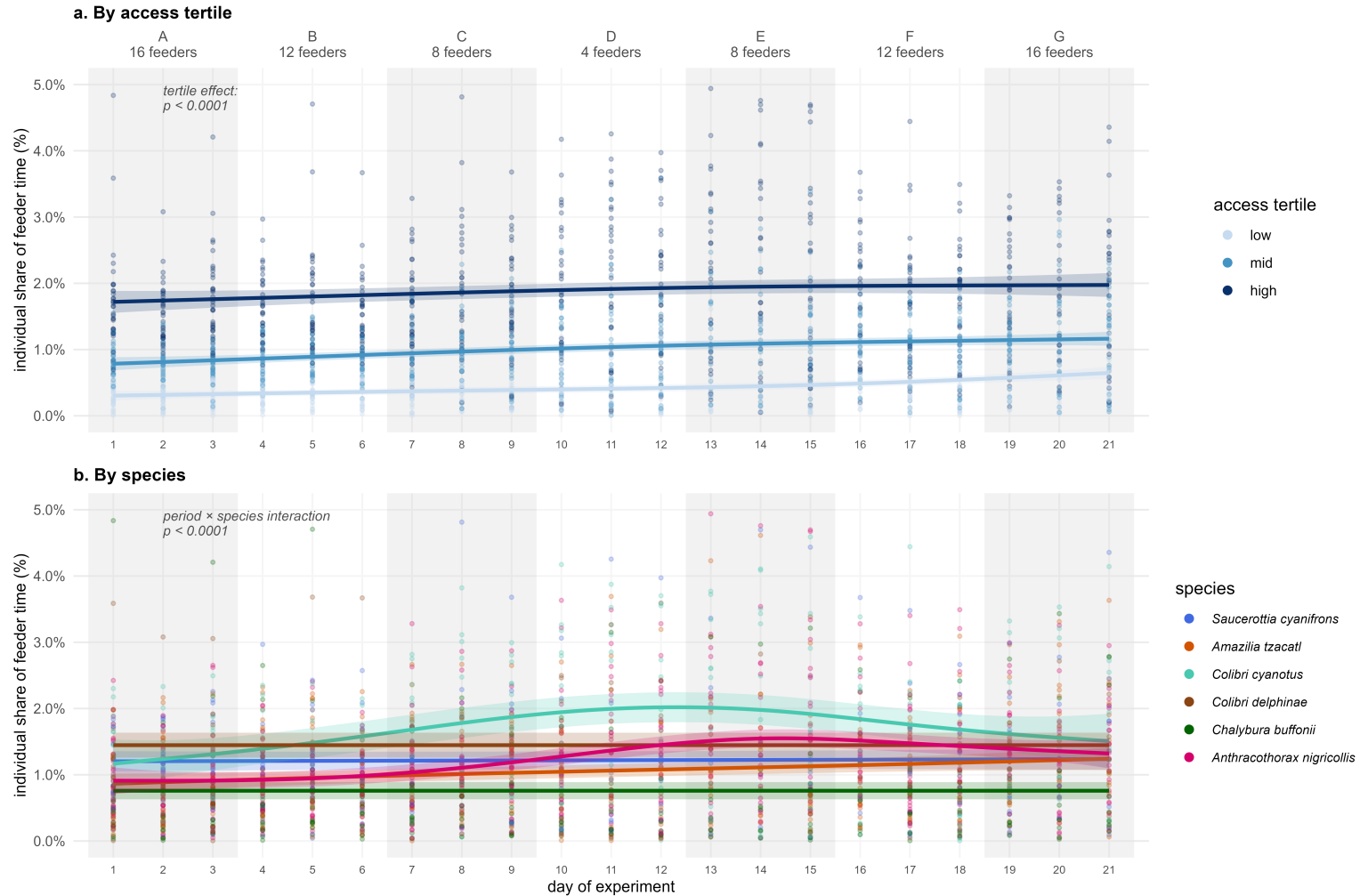


Figure 4. Individual relative access to feeders across the experiment. Each point represents each bird's share of each day's total feeder time (with all birds summing to 100%—note that equal sharing across all 109 birds would allot each individual ~0.9%); trend lines represent generalized additive models (GAM) that flexibly fit group-level trajectories. **(a)** Individual share, stratified by access tertile. High-access birds averaged a 1.69% share of assemblage feeder time, while mid- and low-tertile birds averaged 0.91% and 0.36%, respectively. **(b)** Individual share, stratified by species. *Co. cyanotus* and *Co. delphinae* gained access in periods D–E, while *S. cyanifrons* and *Am. tzacatl* lost access.

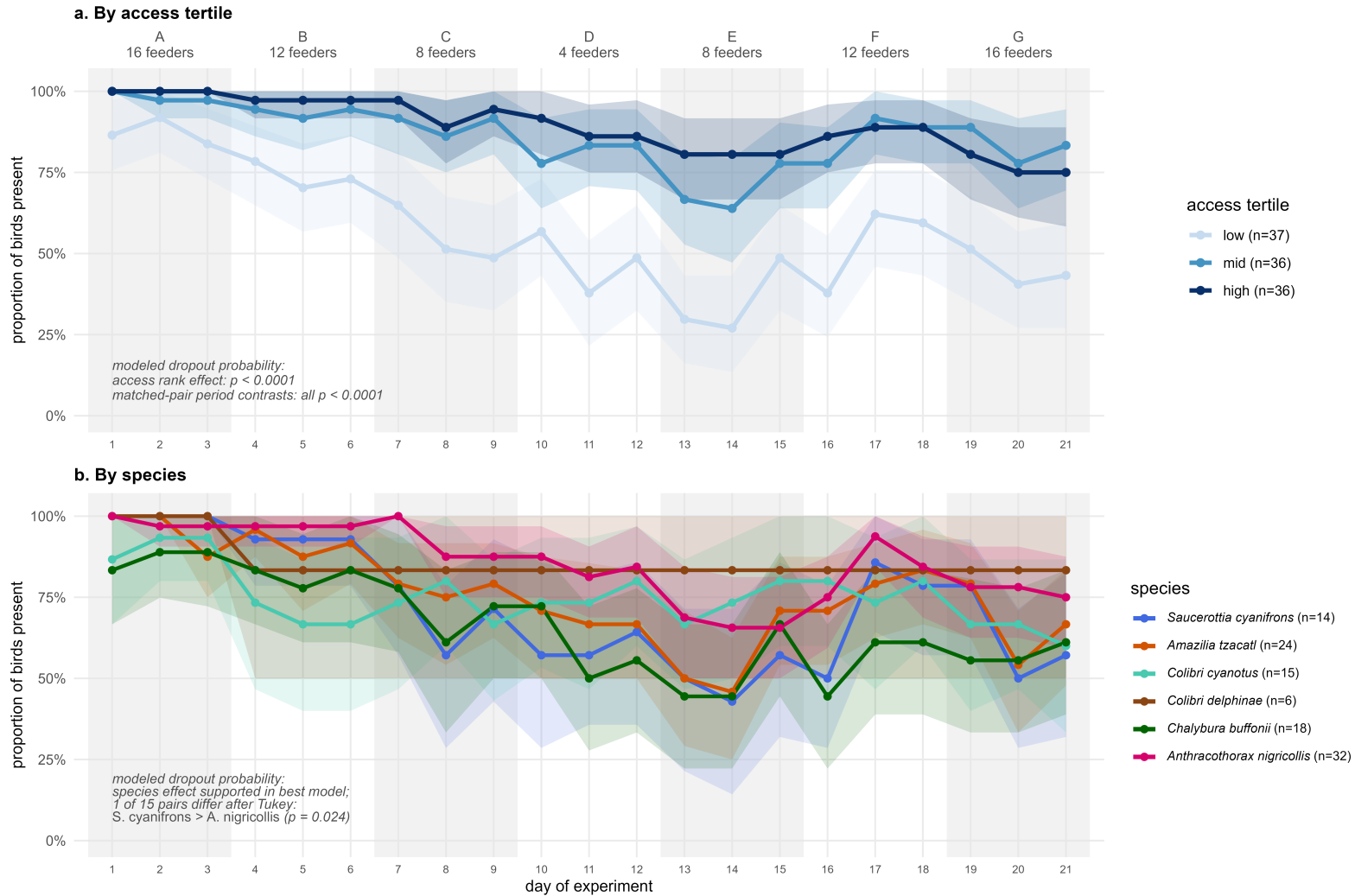


Figure 5. Daily attendance across the experiment. The proportion of birds present each day, split by **(a)** period-A access tertile and **(b)** species. Ribbons show 95% bootstrapped confidence intervals. Low-access birds dropped out significantly more than high-access ones, and there was greater absence in reinstatement periods than in their baseline removal counterparts (i.e., birds did not all return even once we had restored all 16 feeders). Species ranged widely in their predicted absence probabilities, but post-Tukey, only *A. nigricollis* dropped out significantly less often than *S. cyanifrons*.



Figure 6. Foraging windows, morning start times, and evening end times across access tertiles. (a) Each bar is one bird's average first-to-last-visit window across the experiment, sorted by time of first visit. High-access birds occupied wider windows that extended towards dawn and dusk, while low-access birds concentrated their visits around midday. (b, c) Average last-visit and first-visit timestamps, respectively, across the 21 days. Panels (b) and (c) apply an “each-side-of-noon” rule: last-visit times include only bird-days with activity past noon, and first-visit times include only bird-days with activity before noon. Low-access birds ended earlier than high-access birds in every period (all $p \leq 0.008$) and started later than both mid- and high-access birds during baseline, scarcity, and late reinstatement. High-vs.-mid contrasts were significant only in periods C and D.

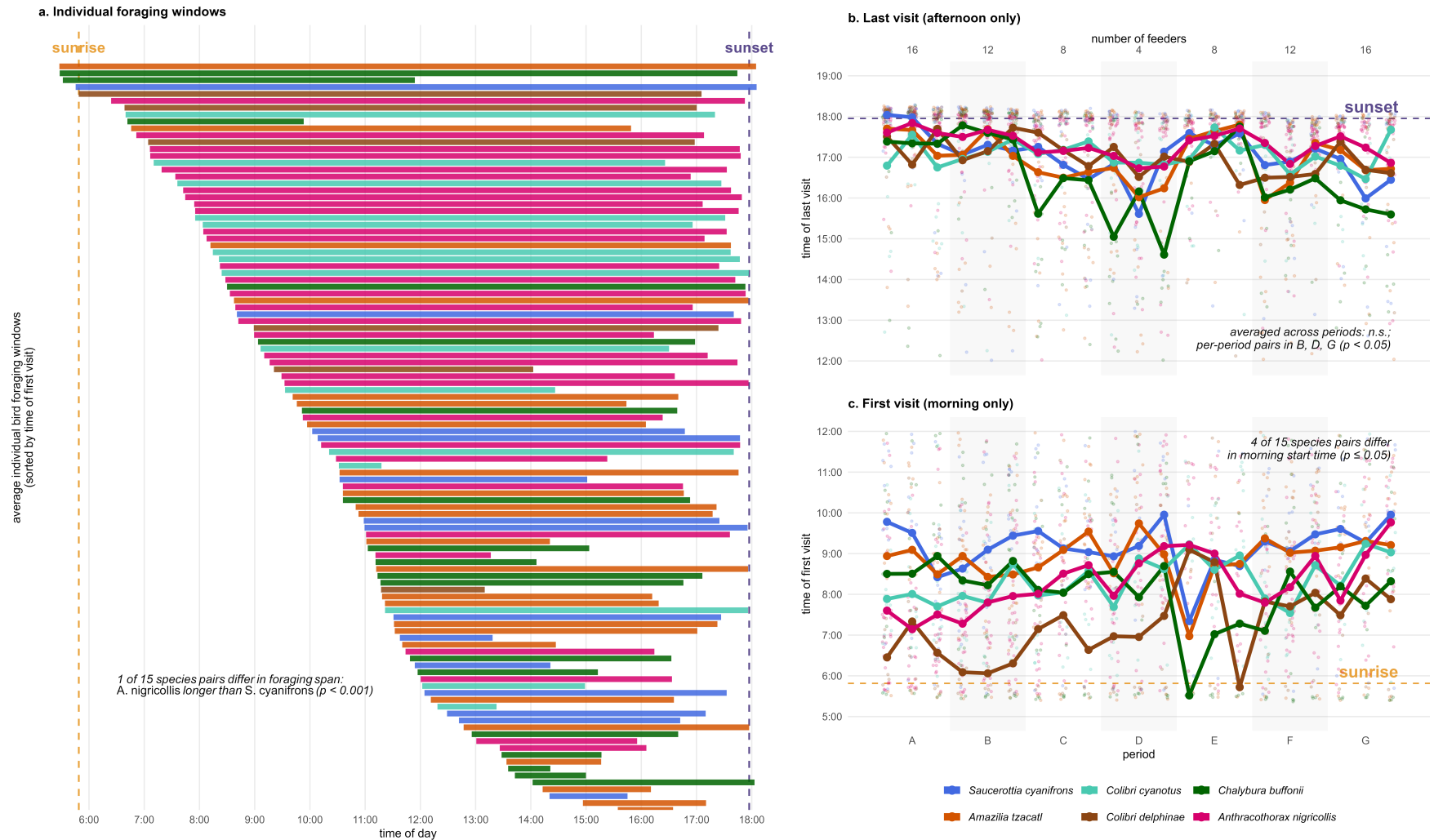
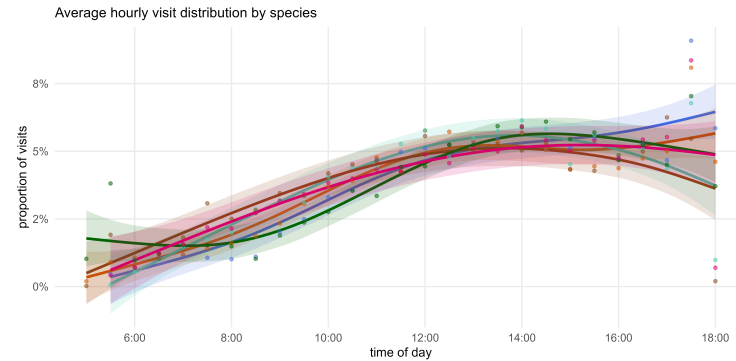
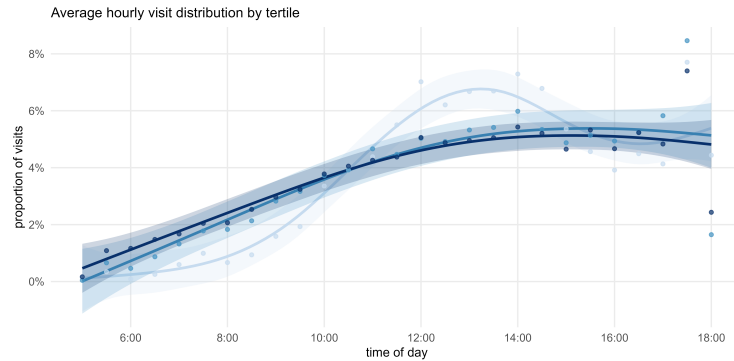


Figure 7. Foraging windows, morning start times, and evening end times across species. (a) Each bar is one bird's average first-to-last-visit window across the experiment, sorted by time of first visit. *An. nigracollis* had significantly wider windows than *S. cyanifrons*. (b, c) Average last-visit and first-visit timestamps, respectively, across the 21 days. Panels (b) and (c) apply an “each-side-of-noon” rule: last-visit times include only bird-days with activity past noon, and first-visit times include only bird-days with activity before noon. In the mornings, *S. cyanifrons* started later than *An. nigracollis*, *Ch. buffonii*, and *Co. delphinae* (all $p \leq 0.046$), and *Am. tzacatl* started later than *Ch. buffonii* ($p = 0.04$). Averaged across periods, end-of-day timing did not differ significantly among species in afternoon-restricted data, but some pairs were significant in specific periods.

a. hourly visit distribution



b. temporal partitioning across periods

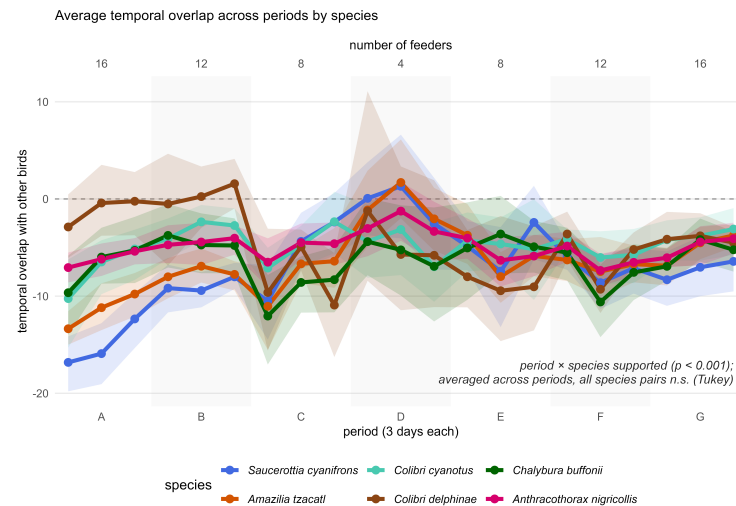
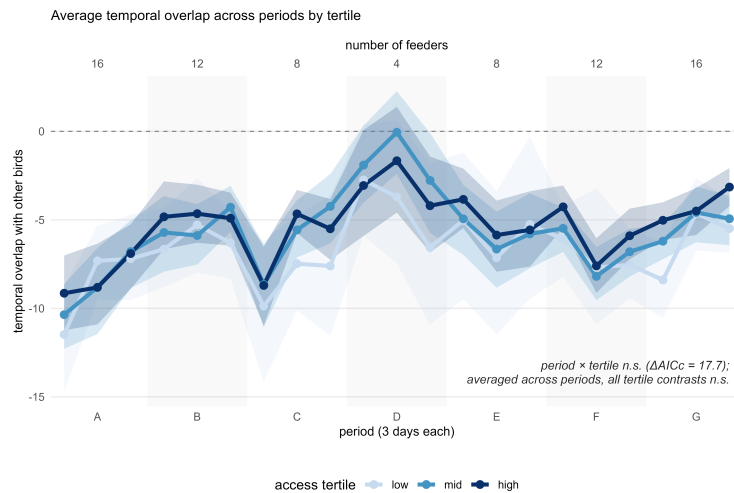


Figure 8. Temporal foraging across access tertiles (left column) and species (right column). (a) Hourly distribution of visits across the day, shown as the proportion of each group's visits falling into each 30-minute bin; smoothed trend lines are GAM fits. The temporal pattern was largely overlapping across tertiles and species. (b) Temporal overlap under our spatiotemporal partitioning index. Negative values indicate more co-occurrence with other birds than random draws of feeder and visitation time would predict. Colored lines show group daily means with 95% bootstrapped CIs (500 replicates) across the 21 days. Temporal overlap peaked closest to zero (least co-occurrence above random expectations) in period D. Access tertile did not factor into the main model (additive term nearly tied, $\Delta AICc = 0.91$), but here we show the rejected period*access term ($\Delta AICc = 17.7$) for visual clarity. Species differed most in periods A and B, but that variation shrank under scarcity.

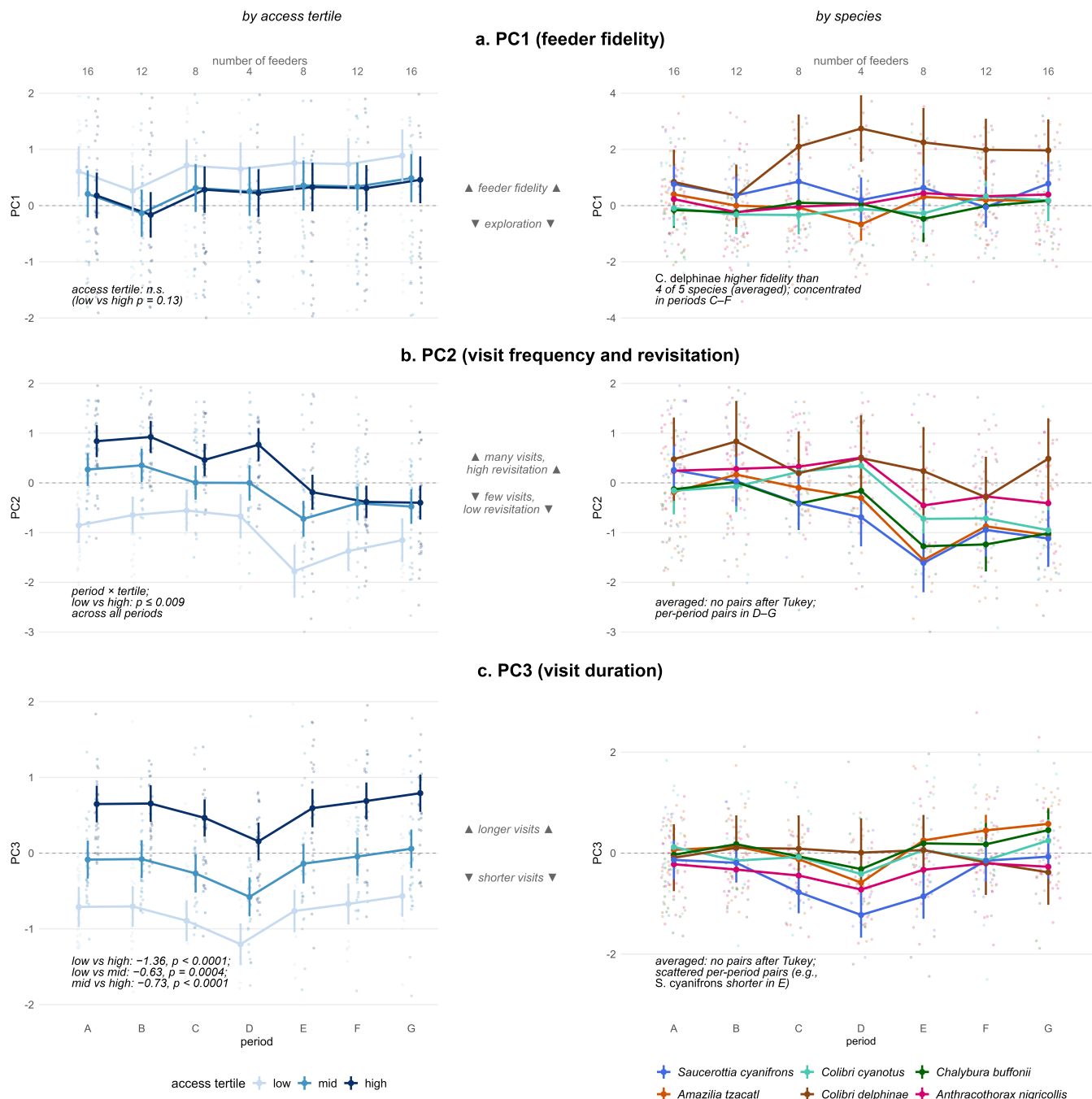


Figure 9. Foraging strategies across periods on three principal-component axes. Average PC scores of access tertiles (left column) and species (right column), with 95% CIs from mixed-effects models; dots show individual bird-period means. **(a)** PC1 (feeder fidelity vs. exploration) had no tertile effect after controlling for species; *Co. delphinae* was an outlier with high feeder fidelity in periods C–F. **(b)** PC2 (visit frequency and revisitation) had a strong period*tertile interaction, with high-access birds consistently scoring higher (more visits, more revisitation) than low-access birds in all periods; species pairs emerged in periods D–G. **(c)** PC3 (visit duration) captured variation separate from PC2; high-access birds made longer visits than low- and mid-access birds across the experiment, and there were only significant species pairs in scarcity and reinstatement periods.

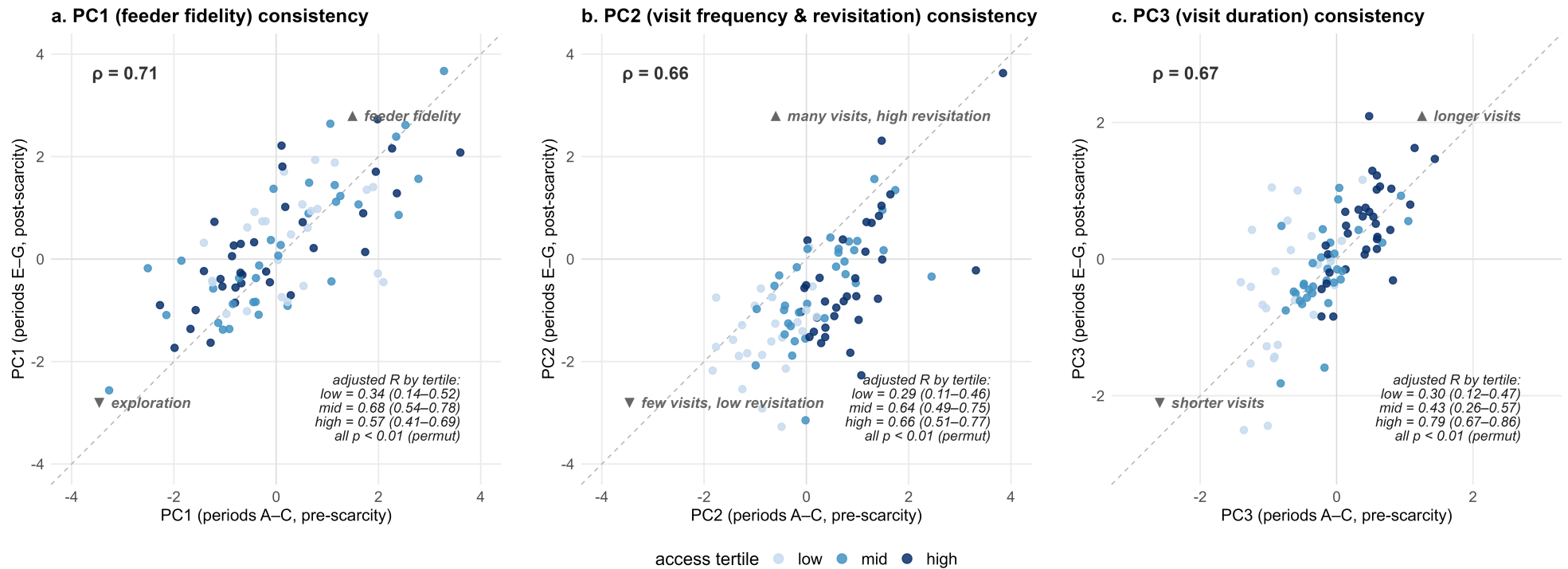
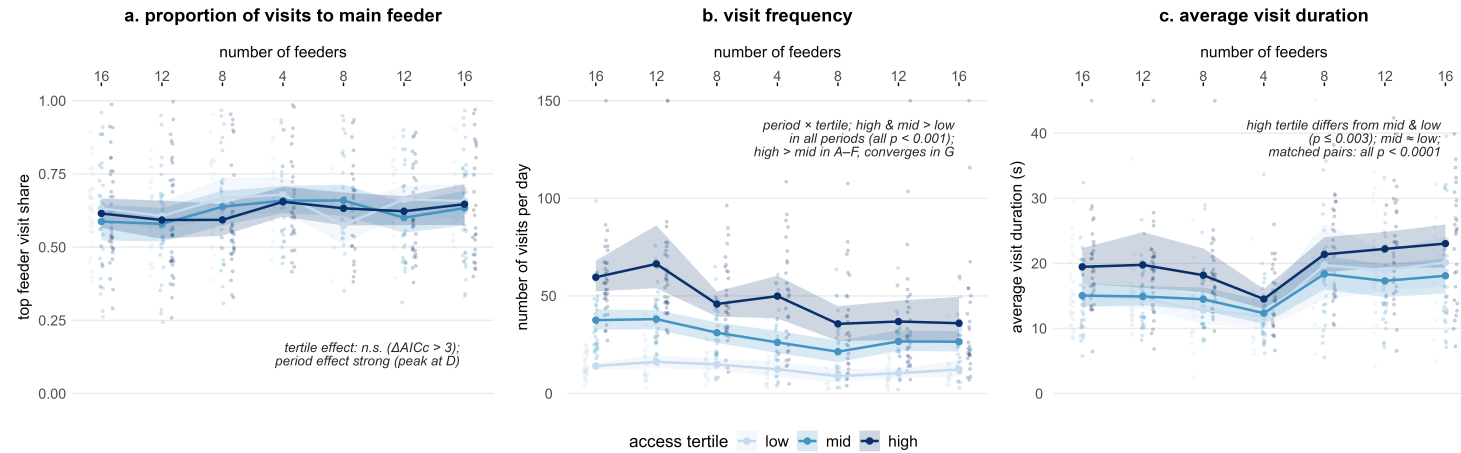


Figure 10. Individual foraging strategy consistency before and after scarcity. Each point represents one bird, colored by its period-A access tertile and positioned by its mean principal component score during the removal arc (x-axis, periods A–C, 16–8 feeders) and the reinstatement arc (y-axis, periods E–G, 8–16 feeders). Points exactly on the diagonal represent birds that returned to their pre-scarcity value; points above the diagonal are birds that shifted upward on the PC; points below are birds that shifted downward. **(a)** PC1 (feeder fidelity): birds exhibited a modest overall shift upward, indicating that the population drifted slightly towards more feeder-faithful patterns after scarcity. **(b)** PC2 (visit frequency and revisitation): with nearly all points below the diagonal, birds shifted toward fewer visits with less revisitation after scarcity. **(c)** PC3 (visit duration): birds exhibited another modest upward shift, indicating that the population trended slightly towards longer visits after scarcity. Low-tertile birds were roughly half as repeatable as mid/high birds on PC1 and PC2, with the span widest on PC3 ($R = 0.30$ low-access, 0.43 mid-access, and 0.79 high-access).

by access tertile



by species

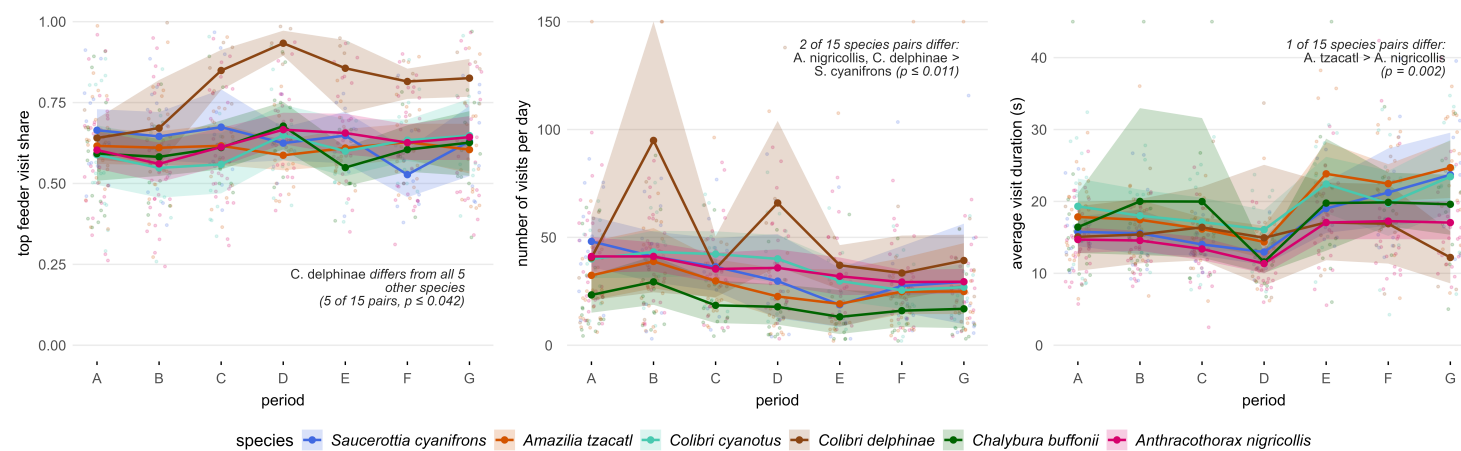


Figure 11. Raw foraging metrics across the experiment, by access tertile (top row) and species (bottom row). Each foraging metric contributed to one of the three principal-component axes: **(a)** proportion of visits to main feeder (PC1), **(b)** visit frequency (PC2), and **(c)** average visit duration (PC3). Points represent individual bird-period averages; lines represent each group's period mean with 95% bootstrapped CIs (500 replicates). Favorite feeder proportion did not significantly differ between access tertiles, but *Co. delphinae* had significantly more concentrated visits than all other species. High- and mid-access birds had significantly greater visit frequency than low-access birds, as did *An. nigracollis* and *Co. delphinae* over *S. cyanifrons*, while high-access birds had significantly longer visits than mid- and low-access birds, as did *Am. tzacatl* over *An. nigracollis*.

Supplementary materials

Supplementary methods and results

S1. Q1 extension: additional competition under scarcity analysis

In addition to *traffic pressure* (as defined in the main methods), we calculated two complementary, site-wide crowding metrics based on the visits logged at each feeder each hour: **(1) time pressure**, total time in seconds—a time-based equivalent to traffic pressure; and **(2) occupancy pressure**, the number of unique individuals detected, which lets us distinguish between “one bird visiting many times” (high traffic pressure, low occupancy pressure) and “many different birds visiting” (high traffic and high occupancy pressure). As with traffic pressure, we also scaled both metrics by dividing the daily totals by the number of feeders that were available.

Both metrics were highly correlated with traffic pressure across the experiment: time pressure at Spearman’s $\rho = 0.957$, and occupancy pressure at $\rho = 0.921$ (these two metrics were also highly correlated with each other at $\rho = 0.907$). Both time and occupancy pressure exhibited similar trends across the experiment, with a peak in period D and then a drop to or below removal arc levels throughout the reinstatement arc. Because of the strong correlation between the three metrics, we elected to report only traffic pressure in the main results.

S2. Q4 extension: additional feeder preference and community turnover analysis

Feeder preference. Given that raw visit proportions can be misleading without accounting for feeder availability—e.g., visiting one of two feeders 50% of the time does not necessarily signify equal preference as visiting one of 16 feeders 50% of the time—we also calculated an availability-corrected *preference index* for each bird-feeder-day with Chesson’s α (Chesson 1978, 1983). Here, α represents the ratio of observed vs. uniform expectation (with “observed” being how much a bird actually used a feeder, and “uniform expectation” being how much the bird would have used the feeder if it spread all of its visits evenly across the available options): values of 1 indicate use that is proportional to availability, values > 1 indicate preference, and values < 1 indicate avoidance (as similarly applied in Cloyd & Eason 2017). We then normalized these values across the number of available feeders, such that values summed to 1 per bird-day, in order to properly compare between bird-days that had different feeder counts.

Across all bird-days of the experiment ($n = 2,289$), preferences averaged at 0.67 (with a median of 0.65)—well above that expected under uniform use. Like with “favorite feeder proportions” in Q7, the preference index rose from 0.64 in period A to 0.73 in period D, then remained high throughout the reinstatement arc (e.g., period G: 0.69). At the bird level, mean preference index and PC1 score (from Q6) were strongly correlated (Spearman’s $\rho = 0.894$, $n = 108$) at the bird level. Thus, feeder preferences did in fact elevate during scarcity, without simply being a methodological artifact of availability.

Community turnover at the feeder level. Our recruitment analysis revealed 9 birds that were present in period G but not period A, which, all told, comprised 8.9% of the 101 birds active in period G (with no data filters applied) and included 4 *Co. coruscans*. These “recruits” were modestly active (with a median of 18 visits in period G vs. 51.5 visits for the 92 individuals detected in both periods) and contributed to only a small portion (mean 2.6%) of the per-feeder

visits in period G. Recruits therefore did not meaningfully account for the turnover that we observed at feeders.

S3. Q5 extension: additional dawn/dusk sensitivity check for partitioning analysis

Our midday subset analysis supported the full-day findings that we present in the main text. For observed crowding, the tertile contrast between high- and low-access birds remained significant ($p = 0.0052$). For spatiotemporal partitioning, the grand mean was very similar at ~5.45 more tagged birds at the same 30-minute feeder window than would be expected under random feeder choices and visit timings, tertile effects remained non-significant, species still varied in their clustering when resources were abundant, and three of the four period contrasts remained significant (just C vs. E lost significance, $p = 0.23$). All told, the consistency across the two datasets suggests that our Q5 findings are not simply an artifact of circadian-driven crowding at sunrise and sunset.

S4. Q6 extension: additional PC metrics and SD companions

Feeder-use inequality. We also calculated *feeder-use inequality*: the Gini coefficient of a bird's daily visit distribution across the available feeders (cf. Tenczar et al. 2014, Rotics & Clutton-Brock 2021). As with competition inequality, values ranged from 0 (entirely even visits across feeders) to 1 (all visits to a single feeder). In order to properly differentiate between a bird unevenly visiting just a few vs. many feeders (e.g., concentrating most visits on one of two feeders vs. one of 12 feeders would both return a high Gini coefficient), we included unused but available feeders as zeroes in our calculation. Ultimately, however, we elected to exclude this metric from our PCA, as it correlated strongly ($r = -0.82$) with our feeder-use entropy metric.

Bird-level PC1 SD as a companion to PC repeatability. To explore each bird's variability in feeder fidelity, we calculated individual standard deviations in PC1 scores across periods (both raw and after subtracting the mean period effect, in order to isolate the variation specific to individuals), only including birds that were present for at least 3 periods ($n = 96$). These standard deviations ranged from 0.27–1.70 when raw (with a median of 0.86) and from 0.26–1.62 (with a median of 0.82) when adjusting for period. The two were very strongly correlated ($r = 0.97$)—i.e., removing the period signal made very little difference to individual variability, which is consistent with the fact that PC1 values were nearly identical when we did and did not adjust for period (difference of 0.008) in our repeatability analyses. Similarly to the small amount of interspecific variation in individual PC1 consistency that we report in the main text, we also found little intraspecific variation here: mean residualized SDs ranged from 0.78–1.12 within all species.

Supplementary literature cited

- Chesson, J. (1978). Measuring preference in selective predation. *Ecology*, 59(2), 211–215.
- Chesson, J. (1983). The estimation and analysis of preference and its relationship to foraging models. *Ecology*, 64(5), 1297–1304.
- Cloyed, C. S., & Eason, P. K. (2017). Niche partitioning and the role of intraspecific niche variation in structuring a guild of generalist anurans. *Royal Society Open Science*, 4(3), 170060.
- Rotics, S., & Clutton-Brock, T. (2021). Group size increases inequality in cooperative behaviour. *Proceedings of the Royal Society B: Biological Sciences*, 288(1959), 20202104.
- Tenczar, P., Lutz, C.C., Rao, V.D., Goldenfeld, N., & Robinson, G.E. (2014). Automated monitoring reveals extreme interindividual variation and plasticity in honeybee foraging activity levels. *Animal Behaviour*, 95, 41–48.

Supplementary tables

Table S1. Activity at feeders during each period. *Active birds* (individuals registered at feeders each day) and *active feeder-hours* (total feeder-hours with at least one registered visit each day) columns are calculated across the three days within each period. The *percent use* sub-column represents the following calculation: (mean active feeder-hours) / (number of feeders × 14 possible diurnal hours) × 100.

Period	Feeders	Active birds (range)	Active birds (mean)	Active feeder-hours	
				Mean	Percent use
A	16	102–105	104.3	170.3	76.0
B	12	94–98	96.0	151.7	90.3
C	8	82–92	86.3	100.7	89.9
D	4	75–82	78.7	55.0	98.2
E	8	62–75	67.0	91.3	81.5
F	12	73–88	82.3	111.0	66.1
G	16	70–80	74.3	138.3	61.7

Table S2. Mean time (in seconds) spent by species at available feeders during each period, averaged across each visitor's three-day average. Rows are sorted by descending period A total time; see column headers for the number of feeders in each period.

Species	A (16f)	B (12f)	C (8f)	D (4f)	E (8f)	F (12f)	G (16f)
<i>Colibri cyanotus</i>	773	780	746	613	623	529	556
<i>Colibri delphinae</i>	762	1,099	567	615	443	479	444
<i>Saucerottia cyanifrons</i>	752	660	555	293	310	431	402
<i>Anthracothonax nigricollis</i>	597	585	453	391	519	489	483
<i>Amazilia tzacatl</i>	508	621	473	279	294	417	416
<i>Chalybura buffonii</i>	491	522	297	181	172	231	323

Supplementary figures

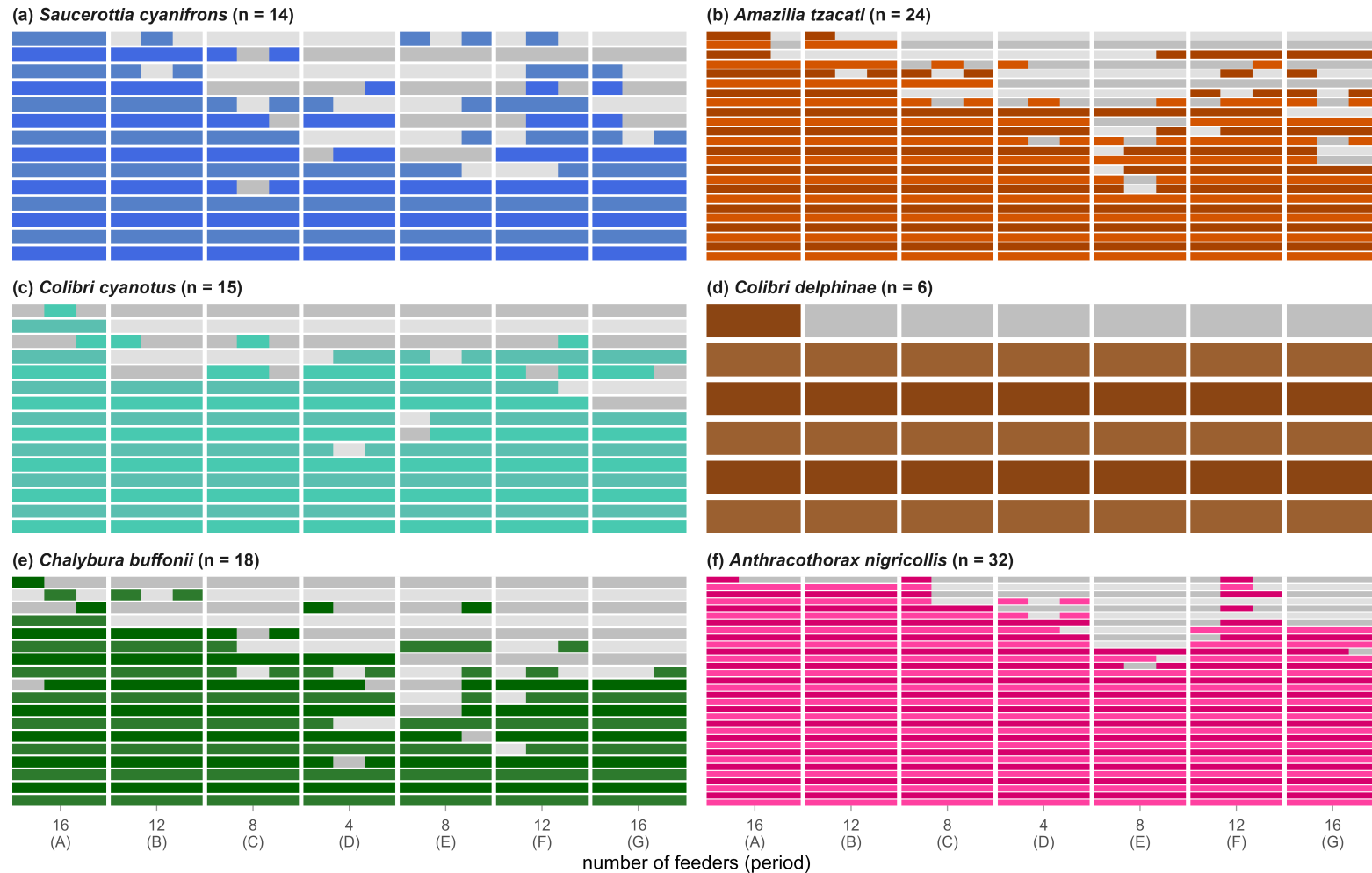


Figure S1. Individual attendance heatmap, across the 21-day experiment. Each row is one individual (sample sizes in panel headers) and each column is one day, with periods grouped into three-day contiguous blocks. Colored cells indicate presence (the bird was detected at the available feeders at least once that day) and gray cells indicate absence (no detections). Within panels, birds are arranged by ascending presence (birds detected the fewest days are at the top), and the species panels themselves are arranged by ascending mean body mass (lightest to heaviest).

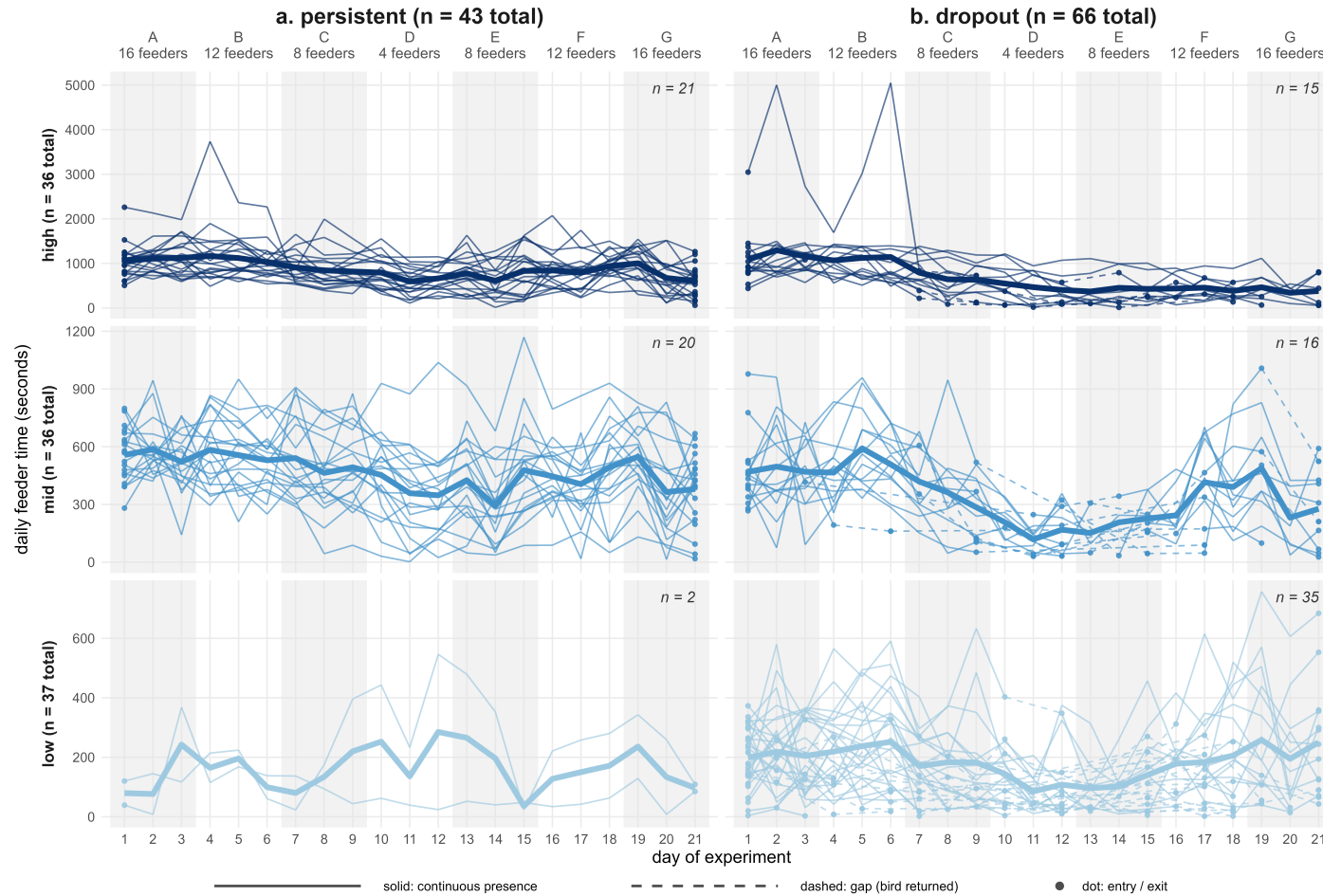


Figure S2. Bird visitation trajectories and dropout by access tertile. The three rows are split by access tertile (high, mid, and low) and the two columns are split into birds that were **(a)** present every day of the experiment (“persistent”); and **(b)** absent on at least one day (“dropout”). Each thin line represents the visit trajectory (daily time spent at feeders across the experiment) of one bird: solid segments indicate contiguous presence, dashed segments span any days when a bird was absent but later returned, and dots mark “entries” and “exits” from the system. Bold lines show the mean visit trajectory of each subgroup. Note that there are no individuals in panel A with dashed absences by definition, and that the y-axes differ by tertile row to better display the variation within each group (absolute visitation time differed by ~5x across tertiles). Dropout varied greatly by access tertile (42%, 44%, and 95% of high-, mid-, and low-access birds dropped out at some point of the experiment, respectively).

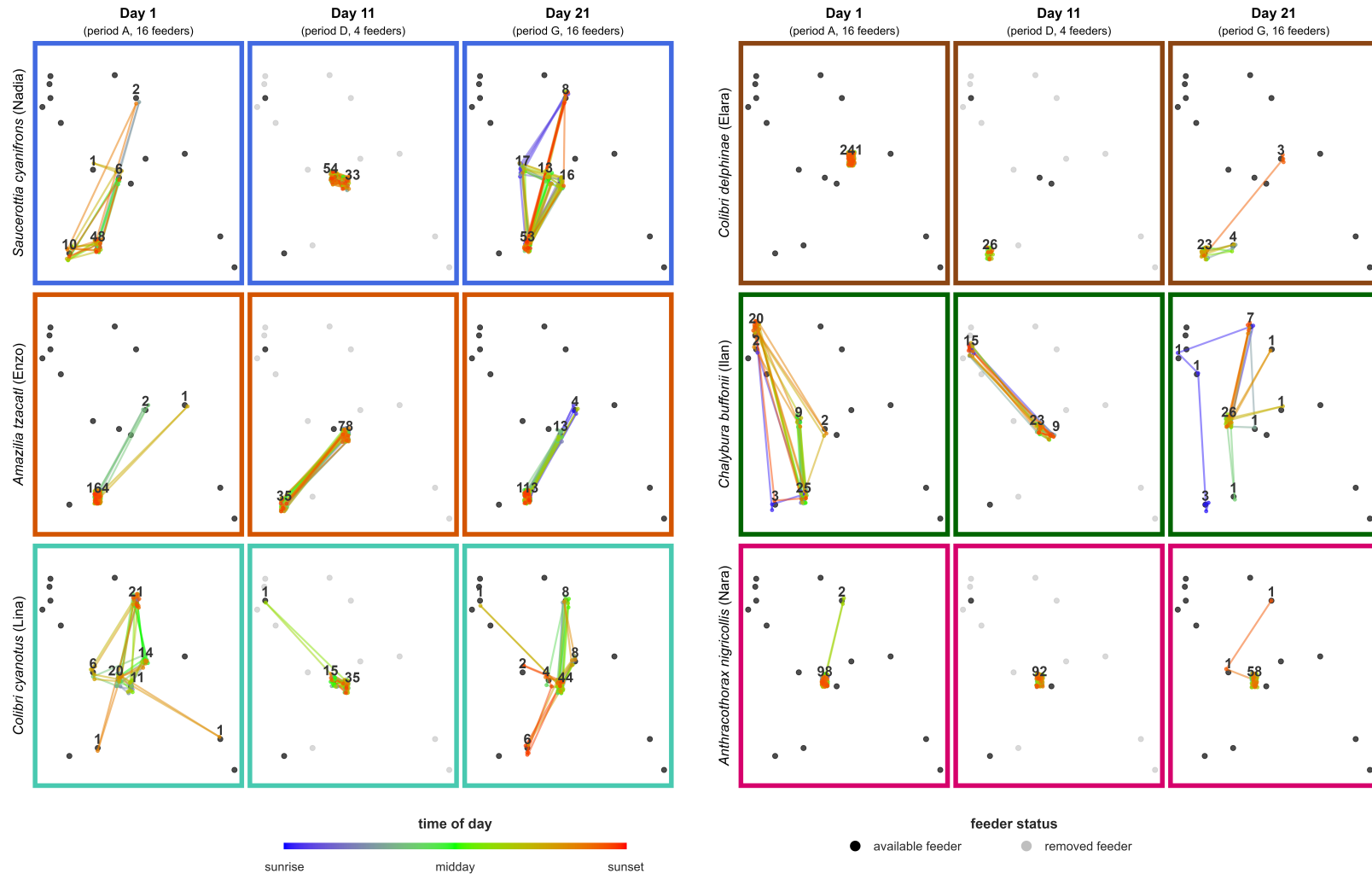


Figure S3. Sample individual foraging maps across the experiment. The visitation patterns of one representative bird per species (the bird present on all 3 target days with the most visits across those days), shown on day 1 (period A: baseline, 16 feeders), day 11 (period D: peak scarcity and midpoint of experiment, 4 feeders), and day 21 (period G: return to full abundance and final day of experiment, 16 feeders). Black points indicate feeders that were active that day; gray points indicate feeders that we had removed. Colored points and lines show each bird's visits and the trajectory between them, with color indicating time of day (sunrise to sunset), and numbers above each visited feeder show how many times that bird visited. Strategies varied within and across individuals and species.

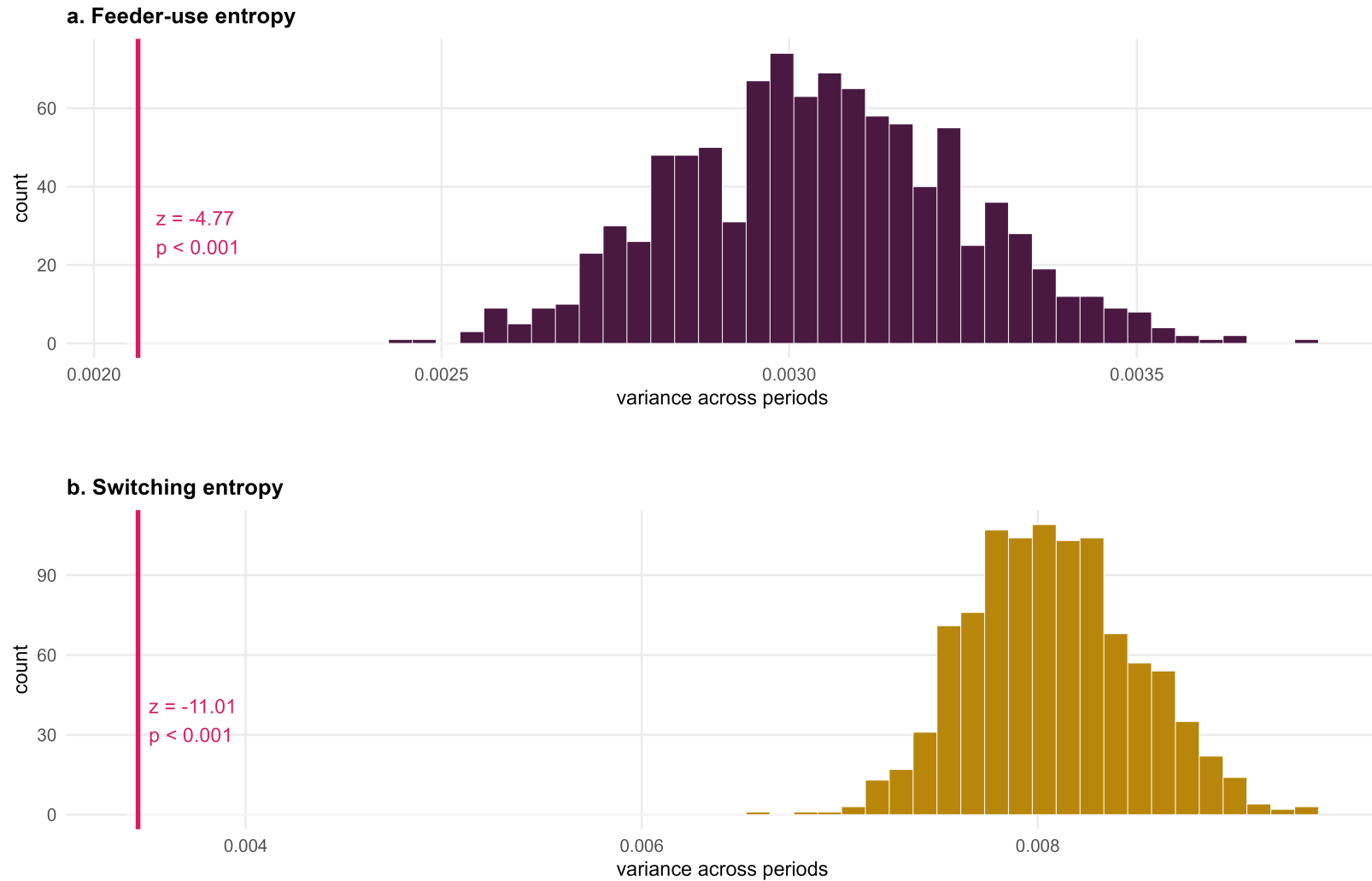


Figure S4. Observed foraging consistency vs. constrained-availability null. (a) Feeder-use entropy: the variance in birds' feeder preference distributions across periods. **(b)** Switching entropy: the variance in birds' feeder-to-feeder transition patterns across periods. The magenta line represents the observed value, while the null distribution had shuffled feeder identity within the available set of units each period ($n = 1,000$ simulations). The negative z-score on each panel indicates that the birds showed more consistent feeder-use and transition patterns than would be expected by chance.

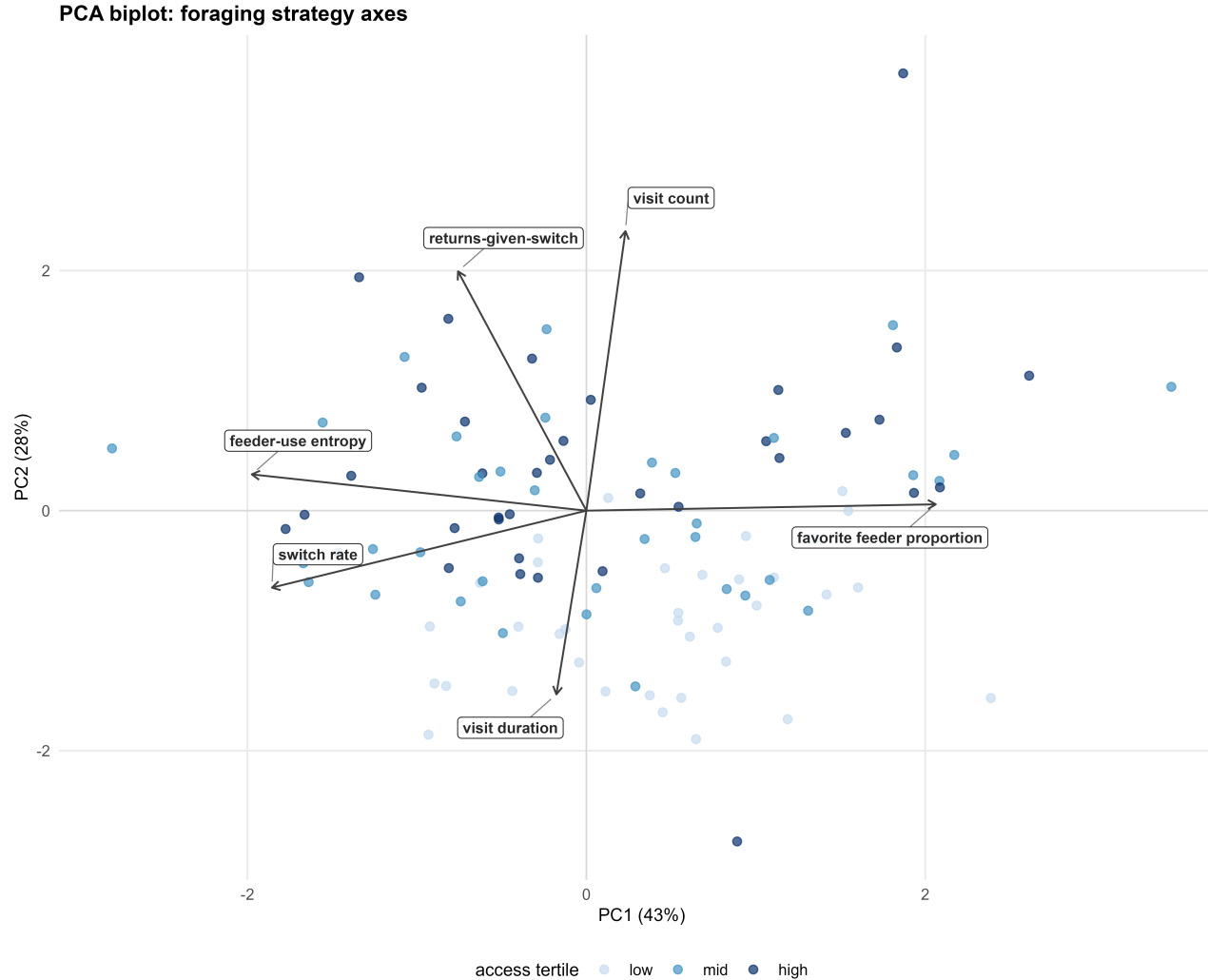


Figure S5. PCA biplot of foraging strategies and its two major axes: feeder fidelity (PC1) and visit frequency and revisitation (PC2). This biplot shows how our six daily foraging metrics loaded onto PC1 (which captured 43% of variance) and PC2 (which captured 28% of variance). Each dot, colored by access tertile, represents one bird's mean PC position across the whole experiment. High PC1 values reflect strong feeder fidelity, whereas low PC1 values reflect more exploratory or diffuse visitation. High PC2 values, on the other hand, reflect many visits with high revisitation, with low PC2 values reflecting few visits and low revisitation. We report PC3 in the main text.