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The Effect of Sexual Dichromatism on Subtle Gender Dimorphisms in Ecuadorian
Hummingbirds

by

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Abstract:

Within the birds there are countless examples of sexual dimorphism, ranging from obvious differences such as in plumage to more discreet variations such as in bill or wing length. The more conspicuous plumage differences are typically attributed to sexual selection, but the evolutionary cause of subtle dimorphisms is much more unclear, with sexual selection and ecological causation both being valid possibilities. Therefore the question arises, are subtle dimorphisms more correlated with species that are already sexually dichromatic, or do both plumage dimorphic and plumage monomorphic species have an equal likelihood of displaying discreet gender differences? To answer this we captured and analyzed fifteen different species of Ecuadorian hummingbirds, six of them being dichromatic, and nine of them being monochromatic. We measured four subtle traits in both genders across all species: weight, wing length, tail length, and culmen (bill) length, and used ANOVAs to determine if there were any significant differences between genders. Our results revealed that dichromatic species do have a greater chance of displaying subtle dimorphisms, with 83% of species having gender differences in at least one subtle trait as opposed to only 44% in monochromatic species. This indicates that there is a correlation between obvious gender differences like plumage and more discreet dimorphisms, although the cause for this, be it sexual selection or ecological causation, remains unclear. However, because some monochromatic species do display significant subtle dimorphisms, we have now opened the door to differentiating gender in these species in the absence of sexual structures.

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Introduction:

Sexual dimorphism, meaning a phenotypic difference in morphology between males and females in a given species, can be seen all across the class of birds. These differences are most notably expressed through variations in plumage (sexual dichromatism), with males often having brighter and more ornamented plumages than females (Bortolotti et al. 1996). Sexual dichromatism was originally explained as a product of sexual selection by Darwin (1871), who theorized that males with brighter and showier plumages could gain more mates through selective advantages in female choice and male to male competition. While showy male plumage may be limited by environmental factors, such as the costs exaggerated colors and ornamentation might incur on predation and parasitism rates (Barraclough et al. 1995), it's still thought to have evolved primarily through sexual selection and social mating systems (Bortolotti et al. 1996; McLain et al. 1999; Dunn et al. 2001; Badyaev & Hill 2003). However, despite a relatively strong scientific grasp on the evolutionary drivers behind dichromatism, the source of more subtle dimorphisms in birds still remains a contested issue (Shine 1989). Some literature suggests that intraspecific niche divergence may be an evolutionary driver behind more discreet sexual differences such as weight and bill length. Males and females may evolve subtle dimorphisms as a result of different feeding regimes and foraging techniques between genders, which in turn reduces intraspecific competition (Shine 1989; Temeles et al. 2000). However, it's inherently difficult to rule out sexual selection, and many studies actually suggest this as the driver behind some subtle dimorphisms (Amadon 1959; Andersson & Andersson 1994; Clark & Dudley 2009). Dunn et al. (2001) found that sexual selection, and more specifically social mating

systems like polygyny, did in fact affect sexual dimorphisms in birds, including subtle gender differences such as weight, wing length, and tail length. These studies suggest a relationship between sexual selection and subtle dimorphisms, and connections between sexual selection and sexual dichromatism have already been drawn (Badyaev & Hill 2003); however it remains unclear if there is a correlation between sexual dichromatism and subtle dimorphisms. The hummingbirds of Ecuador are a good group of organisms to study this in because of their wide range of plumage dimorphism; many species have incredibly dichromatic males and females, while an array of others are so monochromatic that they're currently unsexable in the absence of sexual structures or genetic data (Ridgeley & Greenfield 2001). On top of having many dichromatic and monochromatic species, hummingbirds are also known for often displaying subtle dimorphic differences in features such as bill length or weight (Shine 1989). We will analyze fifteen species of Ecuadorian hummingbirds; six of them being sexually dichromatic, and nine being sexually monochromatic. We will look for significant gender differences in four subtle traits within each species: weight, wing length, tail length, and culmen (bill) length. Because of the relationship between sexual selection and dichromatism (Badyaev & Hill 2003) and between sexual selection and subtle dimorphisms (Dunn et al. 2001), we hypothesize sexually dichromatic species will have a greater likelihood of also displaying subtle dimorphisms, and sexually monochromatic species will be less likely to display them.

Methods:

Description of Study Site:

All of the hummingbirds used in the analysis were caught at one of two locations in Ecuador, either the Loma Alta Ecological Reserve or the Las Tangaras Reserve. The Loma Alta Ecological Reserve is a community owned protected area in the Colonche Hills, near the southwestern coast of Ecuador. The reserve consists of arid dry forest habitat at the lower elevations, but transitions into a cloud forest ecosystem at higher altitudes. The second location, Las Tangaras Reserve, is located in a cloud forest ecosystem near Mindo, in the Pichincha Province of Ecuador.

Field Methods:

The capture and measurement of hummingbirds occurred in the cloud forests of Loma Alta and Las Tangaras, over an eleven year period from 2004 till 2014. Data collection occurred in one to two week periods, typically one to three times each year. To capture the hummingbirds 10 to 20 mist nets were set up over an area of approximately 10 hectares, and were opened in the morning at 6 AM. The nets were then checked every half hour, and any captured birds were removed, placed in clothe bags, and brought back to a central banding station to be banded and measured. At the central banding station each bird was first banded around their right leg, unless they were a recaptured individual, in which case the band number was simply recorded. Afterwards they were then identified to species, sexed, aged, and weighed. The species that were sexually dichromatic were sexed using their plumage (Ridgely & Greenfield 2001). The species that sexually monochromatic could only be sexed if they had identifiable sexual

structures, which could only be found on adults in the breeding season. For males this feature was a cloacal protuberance, a swollen bump on the abdomen indicating the individual was ready for copulation. The sexual feature used for identifying females was a brood patch, an area of bare skin on the breast used for incubating eggs (Pyle & Howell 1997). The absence of either of these features in an individual of a monochromatic species resulted in a gender assignment of “unknown,” making them unusable in later statistical analyses. Next measurements were taken of the wing, culmen (bill), and tail. After these measurements were all recorded, and any notes on molting, diseases, or other conditions were added in, the individuals were then released. If any hummingbird appeared particularly weary or was handled for a longer period of time they were given the opportunity to feed on sugar water before they were released. At 11 AM the nets were closed and the final captured birds were processed. After this all of this information was recorded on a Microsoft Excel spreadsheet

Statistical Analysis:

The statistical analysis began with a Microsoft Excel spreadsheet of every captured individual throughout the eleven year period. The first step was to remove all data points that were not hummingbirds. After this each of the remaining hummingbird species was subjected to sorting, where all the unsexed individuals or duplicate individuals (due to recaptures in the mist nets) were deleted. After this was completed any hummingbird species that had fewer than 10 unique and sexed individuals was subsequently removed from the analysis. Next each species and all of its relevant data points (gender, weight, wing length, tail length, and culmen length) were imported into Minitab 17 Statistical Software. Then each of the four trait measurements were run

though a one-way analysis of variance (ANOVA), where the response was the trait (i.e. tail length) and the factor was the gender. From this output the mean and standard deviation was recorded for each gender for the given trait, as well as the final P-value.

Results:

The p-values derived from the ANOVA were analyzed under a 95% confidence interval, so any values at .05 or less were accepted to be statistically different. Out of the fifteen species analyzed, 60% were found to display subtle gender differences in at least one trait (see Table 1). Of the plumage dimorphic species, 83% displayed gender differences in at least one subtle trait. However in the plumage monomorphic species, only 44% of species displayed one or more subtle gender differences. In total, 75% of all subtle gender differences were found within dichromatic species, with the other 25% being attributed to monochromatic species. Of the four traits analyzed, tail length was most often statistically different in gender, with differences being found in 47% of all species analyzed. Next was culmen length at 33%, followed by wing length and weight, both at 27%.

Table 1: A chart showing each hummingbird species, their presence of dichromatism, and their respective P-values for each of the four traits studied. Blue cells indicate there was a significant difference with the larger value attributed to the male, orange cells indicate significant differences with the larger value attributed to the female.

Species	Dichromatic	Weight	Wing	Tail	Culmen
Green-crowned Brilliant	Yes	0.000	0.000	0.000	0.000
Booted Racket-tail	Yes	0.027	0.240	0.000	0.277
Green-crowned Woodnymph	Yes	0.000	0.000	0.000	0.080
Violet-bellied Hummingbird	Yes	0.117	0.291	0.000	0.000
Violet-tailed Sylph	Yes	0.000	0.000	0.000	0.005
White-whiskered Hermit	Yes	0.707	0.130	0.417	0.123
Amazilia Hummingbird	No	1.000	0.348	0.840	0.516
Andean Emerald	No	0.146	0.556	0.011	0.009
Baron's Hermit	No	0.944	0.310	0.341	0.189
Brown Inca	No	0.939	0.317	0.138	0.571
Green-fronted Lancebill	No	0.509	0.050	0.103	0.622
Rufous-tailed Hummingbird	No	0.553	0.332	0.025	0.351
Sparkling Violetear	No	0.099	0.177	0.375	0.000
Speckled Hummingbird	No	0.341	0.773	0.137	0.370
Tawny-bellied Hermit	No	0.818	0.184	0.654	0.140

Discussion:

The Sexually Dichromatic Species:

With 83% of dichromatic species showing subtle dimorphisms, compared to only 44% of monochromatic species, it appears that there is a correlation between sexual dichromatism and subtle gender differences. Sexual dichromatic species that did display discrete gender differences were also more likely to display more of them, averaging 3 out of 4 subtle traits per species compared to just 1.25 out of 4 for sexually monochromatic species.

The question then arises, what is the cause for this correlation between sexual dichromatism and discrete gender differences; does sexual selection affect factors like weight and culmen length just like it affects plumage? Or does having different color patterns in turn cause other discrete traits to evolve differently between genders? Some studies have shown that there are causal relationships between sexual dichromatism and subtle gender differences. Dichromatism often evolves from sexual selection, and this process causes male hummingbirds to be more aggressive towards each other as well as more dominant over females. This male aggression in turn affects foraging behavior, with males defending the best flower patches from other individuals, causing females to forage at less than optimal flowers (Wolf & Stiles, 1970). Because of these different foraging styles, males tend to have shorter bills than females. The shorter bills of the males allow them to feed more efficiently at flowers so they can minimize time spent feeding, and therefore better defend their patches (Temeles, 1996). Females have to travel to more dispersed and less flower dense sources and therefore have longer bills to maximize how much nectar they can draw from flowers, so none is wasted (Bleiweiss, 1999). Within our

study, 67% of sexually dichromatic species with significant differences in bill length had females with longer bills than males, showing some support for this correlation.

While there may be connections between dichromatism and subtle gender differences, these subtle dimorphisms may not necessarily be caused by plumage differences but rather just correlated with them. While the aforementioned study showed a direct relationship with the degree of dichromatism and the degree of bill length dimorphism (Bleiweiss, 1999), other studies suggest subtle gender differences evolve due to sexual selection, as opposed to specifically evolving due to dichromatism. Studies within the birds have found that in sexually selected species, males will often weigh more than females. Males benefit from this larger size because they can more adequately compete with other aggressive males for mates (Amadon 1959; Shine, 1989). Within our own data of dichromatic, and therefore most likely sexually selected (McLain et al., 1999), hummingbirds, 75% of species with significant differences in weight had the male as the heavier gender, showing some support for the relationship between weight and sexual selection.

Tail length differences in gender has also been linked to sexual selection in birds, with males often evolving longer tails in order to more successfully court females (Clark & Dudley, 2009). This agrees well with our data; all five of the sexually dichromatic hummingbirds that showed significant differences in tail length had males with longer tails than females. Interestingly enough, the gender differences in tail length in these hummingbirds may in turn be driving their gender differences in wing length. Studies have shown that to mitigate the aerodynamic cost of long, sexually selected tails, males have also increased wing size to help decrease wing loading and make flight more

manageable (Andersson & Andersson 1994). This may have played a role with the hummingbirds we studied as well, given that of the sexually dichromatic hummingbirds that had significant differences in both tail length and wing length, 100% had males as the gender with greater tail and wing length. However, it's also possible that the differences in wing length evolved in connection to sexually selected increases in male size, as larger birds have been shown to subsequently have longer wings to help handle their increased weight (Andersson & Andersson, 1994). Within our data we found that all sexually dichromatic hummingbirds that had significant gender differences in both weight and wing length had the males with the greater weights and wing lengths. Because of these findings it's uncertain if wing length dimorphisms in the sexually dichromatic hummingbirds we studied evolved due to dimorphisms in tail length, dimorphisms in weight, or perhaps just independently as a result of sexual selection.

The Sexually Monochromatic Species:

Despite the significantly smaller percentage of monochromatic hummingbirds that displayed subtle sexual dimorphisms, it still begs the question: why are these dimorphisms present? It's easy to see how sexual selection could result in both plumage differences and morphometric differences in birds, but its slightly counterintuitive for hummingbirds without plumage differences to still have subtle dimorphisms, even if it was only found in a few of the species we studied. The absence of dichromatism in these species indicates they may not be subject to sexual selection (McLain et al., 1999; Badyaev & Hill 2003), which offers the possibility that the subtle sexual dimorphisms may have arisen through ecological causation instead.

The evidence for ecological causation and intraspecific niche divergence as drivers of sexual dimorphisms in hummingbirds is sparse, not only because of the difficulty in studying hummingbirds but also because it's inherently challenging to rule out sexual selection when looking for evolutionary drivers (Shine, 1989). For instance, sexual weight dimorphism could potentially evolve from three different factors; fecundity selection could cause increased body size in females due to its conferred benefits to breeding success, sexual selection could lead to increased body size in males due to its benefits in male to male competition for mates, or ecological selection could cause size differences due to intraspecific resource competition (Shine, 1989). Because it could also be a complex combination of these factors that's driving weight divergence, it becomes incredibly difficult to determine the actual source of these differences. Within our own research, not a single monochromatic hummingbird showed significant sexual differences in weight, but it does raise the question, are factors besides sexual selection playing a role in the dichromatic species that did show weight dimorphisms?

While the evolutionary driver(s) of weight dimorphisms may be difficult to determine in monochromatic species, it's much more common to find connections between trophic dimorphisms and ecological causation. The connection between hummingbird bill length and the length and width flowers they specialize on has already been drawn (Temeles et al. 2002), and it's further been shown that sexual differences in trophic structure does in fact correlate with sexual differences in foraging behavior (Temeles & Roberts 1993). However, in these studies it remained unclear if ecological causation or sexual selection was responsible for the bill length dimorphisms. While resource partitioning between the sexes is the most probable cause for these differences,

further research is required to ascertain if this, and not sexual selection, is the true driver behind these adaptations (Temeles et al. 2010). However in one hummingbird species, the Purple-throated Carib, it's been shown that floral specialization between sexes, a type of ecological causation, ultimately did drive the sexual dimorphism of bill length (Temeles et al. 2000). Males and females of this species feed on different species of *Heliconia* flowers, and this intraspecific niche divergence has driven each gender to have a different bill length optimized for feeding on their floral specialty. Because of the lack of dichromatism in the Andean Emerald and the Sparkling Violetear, the only two monochromatic species we analyzed to show significant differences in bill length, this ecological causation model may in fact be the reason for these inexplicable differences. Unfortunately there is very little literature on these two species, so further studies in the field would be necessary to better determine the source of these bill length dimorphisms.

Much like weight, tail length and wing length dimorphisms are difficult to trace to ecological causation. But since the four monochromatic species that we found to show these differences don't exhibit apparent evidence of sexual selection (such as dichromatism), what else could drive these dimorphisms? One study presents the possibility of ecological causation for wing length dimorphisms in hummingbirds, suggesting that male hummingbirds evolved shorter wings to more adequately defend dense patches of flowers from conspecifics, while females evolved longer wings for more efficient flight between the undefended but more dispersed flowers (Kodric-Brown & Brown, 1978). However this study goes on to say it's more probable that this wing length dimorphism evolved due to different sexual roles of the male and females, and the impact on foraging behavior is just a byproduct of this. Because of these uncertainties it's

not possible to conclude why monochromatic species exhibit wing and tail differences without further studies into the four hummingbirds we discovered that display this.

Unfortunately it's much harder to draw conclusions about our discoveries of subtle sexual differences in plumage monomorphic hummingbirds. While its possible intraspecific niche divergence could have driven this evolution, it can't be ruled out that sexual selection may've played a role as well, through channels such as breeding behavior or dichromatisms invisible to the human eye (Cuthill et al. 1999). However, our data on monochromatic hummingbird species' subtle dimorphisms does have some distinct benefits, most notably that it allows for identification of males and females that aren't displaying sexual structures. The statistical differences that exist between genders found in some of these plumage monomorphic hummingbirds creates the possibility for the sexing of individuals outside of breeding season, an option not typically available for understudied monochromatic hummingbirds of the neotropics.

Conclusion:

Our study clearly show that there is a correlation between sexual dichromatism and subtle dimorphisms in hummingbirds, but the reasoning behind this correlation is uncertain. Some studies suggest that dichromatism may in turn lead to morphometric gender differences, but others indicate that subtle morphometric features evolve independently due to sexual selection, or even due to the presence of other subtle dimorphisms. To ascertain the true cause behind this correlation would require a case-by-case analysis of each species, but for now the results can only indicate that there is a relationship between sexual dichromatism and subtle sexual dimorphisms. In sexually monochromatic hummingbirds the reasons for the discreet morphometric differences are even more unclear, but our research does allow for the determination gender in some plumage monomorphic species outside of the breeding season.

Literature Cited:

- Amadon, D. (1959). The significance of sexual differences in size among birds. *Proceedings of the American Philosophical Society*, 531-536.
- Andersson, S., & Andersson, M. (1994). Tail ornamentation, size dimorphism and wing length in the genus *Euplectes* (Ploceinae). *The Auk*, 80-86.
- Badyaev, A. V., & Hill, G. E. (2003). Avian sexual dichromatism in relation to phylogeny and ecology. *Annual Review of Ecology, Evolution, and Systematics*, 27-49.
- Barraclough, T. G., Harvey, P. H., & Nee, S. (1995). Sexual selection and taxonomic diversity in passerine birds. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 259(1355), 211-215.
- Bortolotti, G. R., Negro, J. J., Tella, J. L., Marchant, T. A., & Bird, D. M. (1996). Sexual dichromatism in birds independent of diet, parasites and androgens. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 263(1374), 1171-1176.
- Clark, C. J., & Dudley, R. (2009). Flight costs of long, sexually selected tails in hummingbirds. *Proceedings of the Royal Society B: Biological Sciences*, rspb-2009.
- Cuthill, I. C., Bennett, A. T. D., Partridge, J. C., & Maier, E. J. (1999). Plumage reflectance and the objective assessment of avian sexual dichromatism. *The American Naturalist*, 153(2), 183-200.
- Darwin, C. (1871). *The descent of man and, Selection in relation to sex*. London: J. Murray.
- Dunn, P. O., Whittingham, L. A., & Pitcher, T. E. (2001). Mating systems, sperm competition, and the evolution of sexual dimorphism in birds. *Evolution*, 55(1), 161-175.
- Kodric-Brown, A., & Brown, J. H. (1978). Influence of economics, interspecific competition, and sexual dimorphism on territoriality of migrant rufous hummingbirds. *Ecology*, 285-296.
- McLain, D. K., Moulton, M. P., & Sanderson, J. G. (1999). Sexual selection and extinction: the fate of plumage-dimorphic and plumage-monomorphic birds introduced onto islands. *Evolutionary Ecology Research*, 1(5), 549-565.

- Pyle, P., & Howell, S. (1997). *Identification guide to North American birds: A compendium of information on identifying, ageing, and sexing "near-passerines" and passerines in the hand*. Bolinas, California: Slate Creek Press.
- Ridgely, R., & Greenfield, P. (2001). *The birds of Ecuador* (Vol. 2). Ithaca, NY: Comstock Pub.
- Shine, R. (1989). Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *Quarterly Review of Biology*, 419-461.
- Temeles, E. J. (1996). A new dimension to hummingbird-flower relationships. *Oecologia*, 105(4), 517-523.
- Temeles, E. J., Linhart, Y. B., Masonjones, M., & Masonjones, H. D. (2002). The Role of Flower Width in Hummingbird Bill Length-Flower Length Relationships. *Biotropica*, 34(1), 68-80.
- Temeles, E. J., Miller, J. S., & Rifkin, J. L. (2010). Evolution of sexual dimorphism in bill size and shape of hermit hummingbirds (Phaethornithinae): a role for ecological causation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1543), 1053-1063.
- Temeles, E. J., Pan, I. L., Brennan, J. L., & Horwitt, J. N. (2000). Evidence for ecological causation of sexual dimorphism in a hummingbird. *Science*, 289(5478), 441-443.
- Temeles, E. J., & Roberts, W. M. (1993). Effect of sexual dimorphism in bill length on foraging behavior: an experimental analysis of hummingbirds. *Oecologia*, 94(1), 87-94.
- Wolf, L. L., & Stiles, F. G. (1970). Evolution of pair cooperation in a tropical hummingbird. *Evolution*, 759-773.