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Plant and habitat use by Black-breasted Puffflegs (*Eriocnemis nigrivestis*), a critically endangered hummingbird

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ABSTRACT. Black-breasted Puffflegs (*Eriocnemis nigrivestis*) are hummingbirds endemic to Ecuador and are considered critically endangered because of their limited distribution, a population estimated at fewer than 1000 individuals, and ongoing habitat degradation. From November 2013 to June 2016, we examined the foraging preferences of these hummingbirds using a combination of direct observations, time-lapse cameras, and motion-detection software. We first identified 21 species of ornithophilous plants distributed among five sites in the northwestern flanks of the Pichincha volcano in northwest Ecuador. We then monitored these plant species using time-lapse cameras and recorded 144 visits by Black-breasted Puffflegs to seven of the 21 species. Most visits (128 of 144 visits, 89%) were to just two species of plants, *Macleania rupestris* and *Palicourea fuchsioides*, the latter of which is also an endemic and threatened species. In addition, Black-breasted Puffflegs were only observed in the most pristine habitats. Given the potential negative effects of climate change for species in the tropical Andes plus the possible loss and degradation of habitat resulting from human activities, efforts are needed to conserve habitats currently used by Black-breasted Puffflegs, recover degraded habitats, and connect isolated patches of suitable habitat. Our results concerning species of flowering plants used most by Black-breasted Puffflegs (*P. fuchsioides* and *M. rupestris*) should help guide any habitat restoration initiatives.

RESUMEN. **Uso de plantas y habitat por *Eriocnemis nigrivestis*, una especie críticamente amenazada**

Los Calzaditos pechinegro (*Eriocnemis nigrivestis*) son picaflores endémicos de Ecuador considerados en peligro crítico debido a su distribución limitada, una población estimada en menos de 1000 individuos, y a la recurrente degradación de hábitat. De noviembre 2013 a junio 2016, examinamos las preferencias de forrajeo de estos picaflores usando una combinación de observaciones directas, cámaras timelapse, y software de detección de movimiento. Inicialmente identificamos 21 especies de plantas *ornitophilus* distribuidas en cinco sitios en los flancos noroeste del volcán de Pichincha, al noroeste de Ecuador. Luego monitoreamos estas especies de plantas usando cámaras timelapse y registramos 144 visitas por parte del Calzadito pechinegro a siete de las 21 especies. Aun así, la mayoría de las visitas (128 de 144 visitas, 89%) fueron a sólo dos especies de plantas, *Macleania rupestris* y *Palicourea fuchsioides*, siendo la última también una especie endémica y amenazada. Adicionalmente, los Calzaditos pechinegro fueron sólo observados en los hábitats más prístinos. Dado el efecto potencialmente negativo del cambio climático para especies en los Andes tropicales más la posible pérdida y degradación de hábitat resultante de la actividad humana, son necesarios esfuerzos para conservar los hábitats actualmente utilizados por los Calzaditos pechinegro, recuperar hábitats degradados, y conectar parches aislados de hábitat adecuados. Nuestros resultados con respecto a las especies de plantas con flores más utilizadas por el Calzadito pechinegro (*P. fuchsioides* y *M. rupestris*) debería ayudar a guiar iniciativas de restauración de hábitat.

Key words: Ecuador, habitat disturbance, nectar resources, *Palicourea fuchsioides*, restoration, time-lapse cameras

Ongoing climate change and land-use changes threaten many species in the tropical Andes, a global diversity hotspot (Brooks et al. 2002). Hummingbirds in the genus *Eriocnemis* represent one of the most threatened taxa in the high-Andes; of the 12 species in the genus, four are critically endangered and two are considered near threatened (BirdLife International 2017). Black-breasted Puffflegs

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(*Eriocnemis nigrivestis*), endemic to Ecuador and regarded as critically endangered (Birdlife International 2017), have a small global distribution ($\sim$68 km^2) and a population estimated at fewer than 1000 individuals (Jahn 2008). Habitat restoration has been identified as an important strategy for maintaining and increasing populations of Black-breasted Pufflegs (Jahn and Santander 2008). However, to be effective, detailed knowledge of the species ecology, including preferred food plants and possible use of altered habitats typical of the initial phases of restoration, is needed.

Hummingbirds often have preferences for particular plant species and use only a subset of available nectar resources (Vizentin-Bugoni et al. 2014). Trait matching between hummingbird bills and corolla lengths is an important factor that influences patterns of specialization in hummingbird-plant communities (Maruyama et al. 2014, Vizentin-Bugoni et al. 2014, Tinoco et al. 2017, Weinstein and Graham 2017). Currently, little quantitative information is available concerning the plants used by Black-breasted Pufflegs and how floral morphology may influence their foraging preferences. Although the species has been observed foraging on up to 29 species of plants (Bleiweiss and Olalla 1983, Jahn and Santander 2008), these largely anecdotal observations have been made over a period of three decades. Information about which plant species are used most by Black-breasted Pufflegs and how the morphology of their flowers might relate to foraging preferences is still lacking.

Restoring disturbed areas to create suitable habitat for a species requires information about the degree of disturbance the species can tolerate (Marzluff and Ewing 2001). One way to begin to predict if habitat restoration efforts could be successful for Black-breasted Pufflegs is to evaluate the degree to which the species occurs in disturbed areas across the landscape, including forest edges and small forest patches. However, patterns of habitat use by Black-breasted Pufflegs are poorly known. Many hummingbird species are somewhat disturbance tolerant (Stiles 1975), suggesting that disturbed areas may provide suitable habitat for Black-breasted Pufflegs. However, the species appears to be somewhat sensitive to abrupt changes in vegetation cover at a landscape scale, possibly because forest borders impose additional physiological stress on Black-breasted Pufflegs, especially during altitudinal migration (Guevara et al. 2015).

Our study had two main objectives. The first was to understand the foraging ecology of Black-breasted Pufflegs by quantitatively assessing the relative use of available plants and identifying key plant species that might be used in future habitat restoration projects. We further evaluated whether these preferred plants matched the bill length of Black-breasted Pufflegs. Our second objective was to examine patterns of habitat use by conducting observations across habitats that varied in levels of disturbance.

METHODS

Our study was conducted at five sites on the northwestern flanks of the Pichincha volcano, Pichincha province, northwestern Ecuador, covering an altitudinal range of 3252–3541 m (Table 1). The study area lies within the Mindo Important Bird Area (Freile and Santander 2005). Forests in this region are classified as evergreen high-mountain forest of the northern Andes (MDMQ-Secretaría de Ambiente 2011).

We identified four habitat types at our study sites, including (i) large tracts of mature high-Andean forests (hereby, forest) found at Yanacocha and Verdecocha, (ii) a diffuse forest border adjacent to a large area of mature forest and characterized by a gradual transition from forest to shrubby vegetation and then pasture (hereafter, shrubby forest border) located at Esperanza Hill, (iii) a forest border adjacent to a small selectively logged forest patch located next to a pasture (hereby, pastureland forest border) found at Yanacocha, and (iv) a small 0.49-ha forest patch isolated (500 m in straight line) from continuous forest at Yanacocha. We placed transects in each of the five sites (i.e., two in mature forest and one each in the other three habitat types) along existing trails in the forest or along the forest border. Transects varied in length from 0.8–1.5 km and were separated by a minimum distance of 500 m (Table 1).

Plant-bird interaction observations. From November 2013 to June 2014, we identified

Table 1. Coordinates, elevation above sea level, and main habitat category at each study site and transect where Black-breasted Pufflegs and flowering plant interactions were studied using time-lapse cameras

Site	Latitude	Longitude	Transect length (km)	Elevation (m)	Habitat type
Verdecocha	−1.2069 S	−78.59772 W	1.5	3435	Forest interior
Yanacocha forest	−1.2108 S	−78.59028 W	1.2	3541	Forest interior
Yanacocha border	−0.10407 S	−78.59081 W	0.9	3400	Forest border with pastures
Yanacocha patch	−0.10237 S	−78.58908 W	0.8	3400	Forest patch
Esperanza	−0.07258 S	−78.61981 W	1.2	3252	Forest border with shrubs

plants with flowers that might be visited by Black-breasted Pufflegs at Verdecocha where they were commonly observed. For a total of 68 h over 12 d (1–2 d per month) along a 2-km trail, we noted all flowers that exhibited an ornithophilous syndrome (i.e., tubular with bright-colored corollas; Faegri and van der Pijl 1979) and counted the number of times that Black-breasted Pufflegs visited each species of plant per day.

From September 2014 to June 2016, we quantified the number of visits by Black-breasted Pufflegs to flowering plants along each of our five study transects using time-lapse cameras (Plotwatcher Pro, Day 6 Outdoors, Columbus, Georgia). We chose plants based on our earlier observations, as well as those with flowers with clear evidence of the ornithophilous syndrome. We placed up to seven cameras across sites each month, depending on availability of accessible flowers. Cameras were installed at distances ranging from 80 to 100 cm from flowers and were programmed to take a picture every second from 06:30 to 18:30, with a one-hour pause between 12:00–13:00 to avoid overwriting of memory cards. Cameras were removed after 4 or 5 d. We recorded for a total of 1913.9 h across all sites, including 300 h in the Yanacocha forest, 329.6 h at the Yanacocha pasture border, 360.5 h at the Yanacocha patch, 615.5 h, in the Verdecocha forest, and 308.3 h at the Esperanza shrubby border. Because we were interested in the feeding ecology of Black-breasted Pufflegs, we placed more cameras in habitats they commonly used, i.e., forest habitat at Verdecocha and Yanacocha. However, we also obtained 998 h of observations at the disturbed sites. For information about the number of hours we recorded at each species of plant, see Table S1.

Videos were analyzed with Motion Meerkat software (v 1.5; Weinstein 2015). Motion Meerkat is motion-detection software that selects motion-candidate frames from streaming videos. Once the program selected motion-candidate frames, we manually reviewed them to identify hummingbirds. For each species of plant, we determined the total number of visits by Black-breasted Pufflegs. We used two different time intervals between visits, 3 min and 10 min, to define independent visits, and then used these two time intervals to test the robustness of our definition of an independent visit. However, because our results for the two time intervals were similar (Table S2), we only provide data based on the 3-min interval.

Morphological measurements. We measured corolla lengths (± 0.1 mm) of 16 of the 21 plants studied with cameras, with corolla length defined as the distance from the flower opening to the nectar chamber. We also measured the exposed culmen of two museum specimens of Black-breasted Pufflegs deposited at the Ecuadorian Museum of Natural Sciences (MECN) and Museum of Zoology at the Pontifical Catholic University of Ecuador (QCAZ), respectively, and of 13 individuals captured in mist-nets at Yanacocha during May and June 2001 (T. Santander, unpubl. data). Because hummingbirds use their extensible tongues to extract nectar from flowers, we added 33% of the bill length to the total functional bill length (Vizentin-Bugoni et al. 2014, González and Loiselle 2016). We used the difference between corolla length and the

two measures of bill length (bill length alone and with tongues) to explore patterns of trait matching. Values are presented as means ± 1 SD.

RESULTS

During the exploratory phase of our study at Verdecocha, we observed 34 visits by Black-breasted Pufflegs to 14 species of plants. The most frequently visited plants were *Macleania rupestris* (Ericaceae; 3.5 ± 1.0 visits/d and 1.6 visits/h) and *Palicourea fuchsioides* (Rubiaceae; 9.0 ± 2.7 visits/d and 1.3 visits/h).

We monitored 21 species of plants using cameras (Table S1) and recorded 144 visits by Black-breasted Pufflegs to seven species of plants in 58 days of recording (Table 2). Black-breasted Pufflegs were recorded on cameras at just two of our five study sites (Verdecocha and Esperanza) and plants they used at those sites belonged to three families, including Ericaceae (*M. rupestris*, *Thibaudia floribunda*, and *Disterigma alaternoides*), Rubiaceae (*P. fuchsioides*), and Bromeliaceae (*Racinaea tetrantha*, *Guzmania* sp., and an unidentified species of Bromeliaceae) (Table 2). We did not record any flower piercing by Black-breasted Pufflegs.

Overall, *P. fuchsioides* and *M. rupestris* were visited most often by Black-breasted Pufflegs, with the other five species visited only from 1–7 times (Table 2). However, patterns of visitation were not consistent across sites and habitat types (Table 2). For example, *M. rupestris* was the most visited plant at Esperanza, but was not visited at the other sites where it was present. Similarly, *P. fuchsioides* was only visited at Verdecocha.

Corolla lengths of the flowers of 16 of the 21 species monitored by cameras varied from 3.5 mm to 175 mm (mean = 23.6 ± 18.5 mm), and corolla lengths of flowers used by Black-breasted Pufflegs ranged from 8.6 mm to 32.3 mm (mean = 16.3 ± 5.4 mm). Flowers of *P. fuchsioides* and *M. rupestris* best matched the bill length of Black-breasted Pufflegs (Table 2). However, when we added 33% of bill length, the flowers of *P. fuchsioides* best matched the bill and tongue length (Table 2). Detailed information about flower morphology and photos of each flower used by Black-breasted Pufflegs in our study are provided in Appendix S1.

Table 2. Total number of visits and number of visits per hour (in parentheses) by Black-breasted Pufflegs to seven species of flowering plants on the northwestern flanks of the Pichincha volcano in northwest Ecuador, September 2014 – June 2016. Visits were recorded with time-lapse cameras. A 0 indicates that the plant was monitored with a time-lapse camera, but no visits were recorded; a dash indicates that the plant was not found at the site

Plant species	Verdecocha forest	Yanacocha forest	Esperanza shrubby border	Yanacocha pasture border	Yanacocha forest patch	Mean effective corolla ± SD (mm)	Difference between corolla and bill length (mm)	Difference between corolla and bill length + (mm)[a]
Macleania rupestris	0	0	74 (1.6/h)	0	0	17.8 ± 2.1	2.2	−2.9
Palicourea fuchsioides	54 (1.3/h)	0	–	0	0	21.7 ± 3	6.1	0.9
Thibaudia floribunda	7 (0.16/h)	–	–	–	–	16.7 ± 0.7	1.1	−4.1
Unknown Bromeliaceae species	4 (0.08/h)	–	–	–	0	28.3 ± 2.8	12.7	7.5
Guzmania sp.	1 (0.02/h)	0	2 (0.06/h)	0	–	24.9 ± 2.3	9,4	4.2
Disterigma alaternoides	–	0	1 (0.02/h)	–	–	11.5 ± 0.8	−4.1	−9.3
Racinaea tetrantha	1 (0.02/h)	–	–	–	–	12 ± 1.9	−3.6	−8.8

[a]Bill length + tongue (33% of bill length) (Vizentin-Bugoni et al. 2014).

DISCUSSION

Although Black-breasted Pufflegs have been reported to feed on the flowers of a wide variety of plant species (Jahn and Santander 2008), our results suggest that they may concentrate their feeding on certain plants. The most commonly used plant was *P. fuchsioides,* a previously unidentified source of nectar for the species. The flowers of *P. fuchsioides* most closely matched the bill length (including tongue extension) of Black-breasted Pufflegs, suggesting the possibility of some degree of specialization. Trait matching has been suggested as a primary driver explaining specialization in plant-hummingbird networks (Maglianesi et al. 2014, Maruyama et al. 2014, Weinstein and Graham 2017) because such matching may increase the quality of pollination service and the efficiency of nectar intake by hummingbirds (Temeles 1996, Maglianesi et al. 2014).

Flower visitation rates, expressed as hourly visits, varied across plant species. Visit rates for some species of plants were very low (range = 0.02–0.08 visits/h), suggesting that they are less important for Black-breasted Pufflegs. However, visit rates for *M. rupestris* and *P. fuchsioides* were 1.6 and 1.3/h, respectively, and similar to rates reported in the Andean region of Ecuador, including Yanacocha (0.2–2.0 visits/h; Brockmeyer and Schaefer 2012).

Palicourea fuchsioides is an endangered shrub known from only a few locations in the Andes of western Ecuador (Jaramillo et al. 2004). Although not known to occur in any Ecuadorian government protected areas, this shrub could be present in the El Angel Ecological and Cotacachi-Cayapas Ecological reserves (Jaramillo et al. 2004). At our study sites, the plant was present in a ridge-crest elfin forest at Verdecocha where it formed large flowering patches, and was also present at lower densities in mature forest and forest borders at Yanacocha. During our study, *P. fuchsioides* was visited by eight species of hummingbirds, suggesting that Black-breasted Pufflegs are not its exclusive pollinator. Nonetheless, its apparent rarity and importance in the diet of Black-breasted Pufflegs suggest that additional study of its phenology, pollination ecology, and distribution is needed.

We identified four species of plants (including *P. fuchsioides*) that had not previously been reported as sources of nectar for Black-breasted Pufflegs, with three of these in the family Bromeliaceae (*Guzmania* sp., *Racinaea tetrantha*, and an unidentified species). Although the bromeliad species were visited infrequently and their corollas did not match the bill length of Black-breasted Pufflegs, plants in this family might represent supplementary food sources. The bromeliad species along with *M. rupestris*, a plant that was common at all of our study sites and visited frequently by Black-breasted Pufflegs at Esperanza hill, might also provide sources of nectar in disturbed habitats.

Black-breasted Pufflegs were only recorded at two of the three sites with apparently suitable habitat, and they were not recorded in the mature forest at Yanacocha, although they have been observed there previously (Guevara et al. 2015). Forest physiognomy and composition at Yanacocha and Verdecocha were distinct; Verdecocha was characterized by ridge-crest elfin forest with abundant flowering shrubs, and Yanacocha was a hillside forest with a taller canopy and less dense understory. In addition, *P. fuchsioides* was relatively rare at Yanacocha. Whether or not these differences influenced use of these areas by Black-breasted Pufflegs is unclear, but a more detailed examination of the floral composition and vegetation structure of each site is needed to better understand patterns of habitat use. Black-breasted Pufflegs were also observed at Esperanza Hill, a diffuse forest border adjacent to a large mature forest, suggesting that the species might use slightly disturbed habitats. Nonetheless, we did not observe Black-breasted Pufflegs in the two most disturbed habitats (Yanacocha border and patch) even though both *P. fuchsioides* and *M. rupestris* were present and monitored at these sites. These results suggest that Black-breasted Pufflegs might avoid highly disturbed habitats like forest edges that abruptly interrupt otherwise continuous forest habitats (Guevara et al. 2015).

In the face of ongoing climate change, habitats currently used by Black-breasted Pufflegs might be negatively affected if increasing temperatures move the habitable zone for plant species in those habitats above the current timberline (Jahn 2008). In

addition, habitat loss in the region might result in isolated patches that Black-breasted Pufflegs may not use. Under this scenario, efforts to conserve current habitat, recover degraded habitats, and connect isolated patches of suitable habitat might help sustain the species. Information about the plants that appear important for Black-breasted Pufflegs (e.g., *P. fuchsioides, M. rupestris*, and other relatively short-corolla species) should guide future restoration initiatives and propagation techniques. Whether or not Black-breasted Pufflegs switch to other plants during periods of low availability of their preferred plants remains to be determined.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website.

Table S1. Time-lapse camera observation effort invested at each site, habitat, and plant species to record Black-breasted Puffleg visits to flowering plants.

Table S2. Results of Generalized Linear Model analysis of Black-breasted Puffleg daily visit counts to flowering plants and habitat type on the northwestern flanks of the Pichincha volcano in northwestern Ecuador.

Appendix S1. Photo vouchers of the seven plants visited by Black-breasted Pufflegs (*Eriocnemis nigrivestis*) on the northwestern flanks of the Pichincha volcano, northwest Ecuador, November 2013 – June 2016.