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Birdsong tuned to the environment: green hylia song varies with elevation, tree cover, and noise

Alexander N. G. Kirschel,[a,b] **Daniel T. Blumstein,**[a,b] **Rachel E. Cohen,**[a] **Wolfgang Buermann,**[b] **Thomas B. Smith,**[a,b] **and Hans Slabbekoorn**[c]
[a]Department of Ecology and Evolutionary Biology, University of California, 621 Charles E. Young Dr. South, Los Angeles, CA 90095-1606, USA, [b]Center for Tropical Research, Institute of the Environment, University of California, La Kretz Hall, Suite 300, 619 Charles E. Young Dr. South, Los Angeles, CA 90095-1496, USA, and [c]Behavioural Biology, Institute of Biology, Leiden University, PO Box 9516, 2300 RA Leiden, The Netherlands

Animals that communicate acoustically must compete for acoustic space in order to convey their signals effectively. Tropical rainforest birds live in an extremely diverse acoustic community consisting of other birds, mammals, frogs, and many insects. Insects are notable for often producing continuous bands of sound energy at constant frequencies, which vary between species and across habitats. We examined how green hylia (*Hylia prasina*) song frequencies correlate to insect-generated spectral profiles of ambient noise. We also examined how the environment influenced song frequency by using remote sensing to quantify environmental variables. Using path analysis, we assessed the relative effects of elevation, tree cover, precipitation, and insect sounds on green hylia song frequency. Environmental variables were found to directly influence green hylia song frequencies. Specifically, green hylia sang at lower frequencies at higher elevations and under reduced canopy cover. The environment also influenced green hylia song indirectly through its effect on insect sounds. Green hylia sang at lower frequencies presumably to avoid masking by lower frequency insect sounds. Habitat-dependent divergence in songs within species potentially plays an important role in ecological speciation through its impact on species recognition and mate choice. Our data show that factors related to climate, vegetation, and vocal community can promote such habitat-dependent song variation. *Key words:* acoustic adaptation, ambient noise, birdsong, climate, environment, insect sounds. *[Behav Ecol 20:1089–1095 (2009)]*

Tropical rainforests are extraordinarily species rich and consequently extremely noisy (Ryan and Brenowitz 1985; Waser and Brown 1986; Slabbekoorn 2004a, 2004b). The cacophony of acoustic animals in a rainforest generates fierce competition among individuals seeking to transmit their acoustic messages to intended receivers (Planqué and Slabbekoorn 2008). Many bird species sing to defend territories and attract mates (Collins 2004; Catchpole and Slater 2008). In doing so, they must somehow communicate through a diversity of noise levels and spectra of acoustic animals (birds, mammals, frogs, and insects) in their breeding habitat (Klump 1996; Brumm and Slabbekoorn 2005). Abiotic factors also create potential interference. For instance, surf sound from the ocean, stream noise, and wind are examples of continuous noise that can cover much of the sound spectrum, particularly the lower frequencies (Wiley and Richards 1978; Douglas and Conner 1999).

Ambient noise is one factor that may drive birds to sing in a restricted frequency range or move them up or down in frequency use (Ryan and Brenowitz 1985; Slabbekoorn and Smith 2002b). In the rainforest, the predominant, biotic noise source is composed of calling insects, which typically produce sounds of relatively high frequency (Sueur and Aubin 2002; Slabbekoorn 2004a, 2004b). Calling cicadas (Cicadidae), crickets (Gryllidae), and katydids (Tettigoniidae) can lead to consistent differences in ambient noise profiles between rainforest sites (Slabbekoorn 2004a). This is likely due to habitat-dependent changes in species composition or temperature-dependent call frequencies. Crickets and katydids stridulate faster and produce higher frequencies at higher temperatures (Sanborn 2006). In urban environments, the main acoustic problem for singing birds is low-frequency traffic noise. Reports on spectral shifts in urban birdsong in response to anthropogenic noise clearly reveal how singing birds might be capable of adapting their songs to interfering noise levels (Slabbekoorn and Peet 2003; Fernández-Juricic et al. 2005; Wood and Yezerinac 2006).

Sound propagation is a second factor that may shape acoustic design of birdsong (Wiley and Richards 1982). Dense foliage both attenuates and degrades song and favors tonal notes of relatively low frequency and long duration over frequency modulated, rapidly repeated short and high-pitched notes, which are more common in more open habitats (e.g., Morton 1975; Wiley 1991; Slabbekoorn et al. 2002; Blumstein and Turner 2005). Birdsongs may even be adapted to maximize transmission in different forest strata (Nemeth et al. 2001); antbird species (Thamnophilidae) that occur in the densely vegetated forest understory and canopy sing at lower frequencies than close relatives of the more open midstory (Seddon 2005). Thus, geographic variation in density and structure of the vegetation layer typically used for singing and hearing songs may play an important role in signal evolution.

Habitat-specific selection pressures on acoustic signals related to ambient noise and sound transmission have the potential to drive acoustic divergence not only between species (Morton 1975; Ryan and Brenowitz 1985; Wiley 1991) but also among populations within species (Slabbekoorn and Smith 2002b; Slabbekoorn and Den Boer-Visser 2006; Dingle et al.

Address correspondence to A.N.G. Kirschel. E-mail: kirschel@ucla.edu. R.E. Cohen is now at Department of Zoology, Michigan State University, East Lansing, MI 48824, USA

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2008). Such intraspecific vocal divergence may play a critical role in ecological speciation especially when populations are locally adapted and when individuals with distinct songs have also diverged in other fitness-related traits, such as body size, plumage, or bill shape in response to environmental differences (Slabbekoorn and Smith 2002a; Kirschel et al. 2009). Divergence in song features and morphology could be linked, with song divergence occurring as a by-product of morphological adaptation to resources, as found in Darwin's finches (Podos 2001), or divergence in such fitness-related traits could occur independently of each other. Indeed, song frequency has been correlated with body size in birds, with frequency decreasing as body size increases (Ryan and Brenowitz 1985), and this relationship has been found in a *Pogoniulus* tinkerbird along an elevational gradient in sub-Saharan Africa (Kirschel et al. 2009).

Slabbekoorn and Smith (2002b) found that little greenbul (*Andropadus virens*) song had lower minimum frequencies in closed forest sites in Cameroon than in more open habitat sites. This habitat-related shift was correlated to more favorable noise conditions at low frequencies compared with high frequencies in closed forest and more equal noise levels throughout the spectral range of greenbul song in open habitat. *Andropadus virens* also differed significantly in morphology between the 2 habitats (Smith et al. 1997).

However, much of the geographic variation in the little greenbul song, a species that sings songs across a relatively wide frequency band, remained unexplained. Furthermore, the effects of specific climatic and habitat features were investigated to only a limited extent, and these may explain a significant part of acoustic signal structure (Wiley and Richards 1982; Endler 1992; Slabbekoorn 2004a). Birds whose songs utilize a relatively narrow frequency band may be fruitful model systems to understand environmental effects on song because they depend more heavily on tuning into frequency channels of relatively low masking. Remote sensing and climate data have been used to identify how the environment affects species distributions (e.g., Turner et al. 2003; Geffen et al. 2004) and may be used to describe the relationship between vegetation and vocal communities (Ruegg et al. 2006).

Here we examine the impact of elevation, tree cover, precipitation, and ambient noise on geographic variation in the simple, narrowband tonal song of the green hylia (*Hylia prasina*; see Slabbekoorn et al. 2002). We predicted that climatic and habitat features would affect green hylia song frequencies directly, as well as indirectly through their effect on ambient noise profiles. We used satellite imaging and path analysis to examine the direct and indirect impact of all factors together on the spectral variation of green hylia songs. We expected lower frequency green hylia songs where insect sound frequency was lower because green hylia would need to sing at lower frequencies to avoid masking by the noise caused by insects. We expected lower temperatures at high elevations to drive lower frequency insect sounds, thus driving green hylia song lower. We also expected relatively high-frequency songs in more open habitats and that precipitation could also influence song frequencies indirectly via its effect on vegetation type and density and specifically on the assemblages of calling insects found in different habitats.

METHODS

Study species

The green hylia are a monotypic species of Sylvioidea warbler (Sefc et al. 2003). It is a common and widespread species of the midstory of forest habitats in sub-Saharan Africa and has a simple song (Figure 1) comprising 2 whistles given at a constant frequency between 3 and 4 kHz (Slabbekoorn et al. 2002). Although it also produces other calls, we analyzed its song, which is its long distance vocalization (Slabbekoorn et al. 2002) because we expected that song would be most affected by environmental noise and habitat structure.

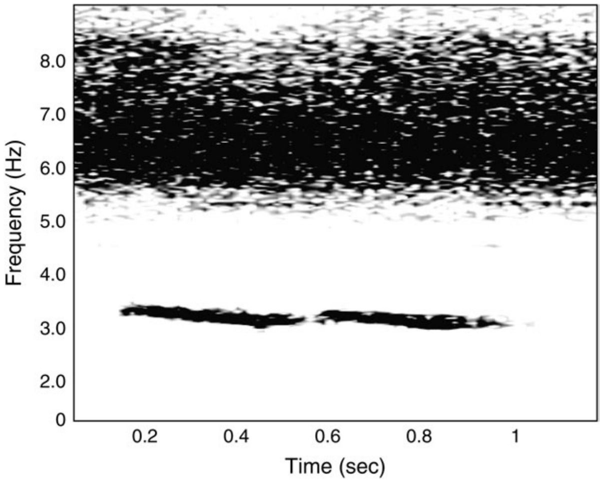

Figure 1
Spectrogram of green hylia song. It comprises 2 notes at a fairly constant frequency, typically between 3 and 3.5 kHz in Uganda. Cicadas are producing sound more than 5 kHz in frequency here.

Recording collection and analysis

We recorded a total of 140 green hylia, of which 66 were recorded using a Sennheiser ME88 shotgun microphone and a Sony TCD5M cassette recorder, between 7 July and 4 September 2004 along forest trails and roads at 11 national parks and reserves in Uganda (see Figure 2). We recorded 74 birds and ambient noise using a Sennheiser ME67 shotgun microphone and a Marantz PMD670 digital recorder at a 44.1-kHz sampling rate between 2 February and 30 September 2007. We aimed to record at least 5 individuals per site but recorded as few as 3 at Queen Elizabeth NP and as many as 27 at Budongo Forest Reserve. We attempted to record at least 3 songs from each individual, but 14 individuals sang just once during recordings and 18 individuals twice. The location of each singing individual was recorded on a Garmin GPS.

Recordings from 2004 were digitized at 16 bits at a 44.1-kHz sampling frequency and saved as AIFF files, using a MOTU 828 soundboard and Raven 1.2 software for sound analyses (Charif et al. 2004). Songs from both 2004 and 2007 were then extracted from each recording and saved as .WAV files for analysis in Raven 1.3 (Charif et al. 2006). The dominant frequency was calculated by taking the mean of the "peak frequency" measurement from the power spectrum of each of the 2 notes. A fast Fourier transformation size of 4096 was used, giving a frequency resolution of 10.8 Hz. We then calculated the mean dominant frequency per individual from the dominant frequencies of each individual's songs. Ambient noise recordings were collected during 2 different seasons (February and September) in 2007 by recording on the hour between 07:00 and 12:00, in 5 directions (north, south, east, west, and directly above) at a constant gain level by setting the gain to maximum, and 1-s samples were extracted and saved as .WAV files from each direction for analysis. We also took GPS measurements of the ambient noise recording locations.

Ambient noise changes in frequency from early morning to midday in these tropical habitats (Slabbekoorn and Smith 2002b; Slabbekoorn 2004a), so in our analyses, it was important to control for any differences in the number of ambient noise

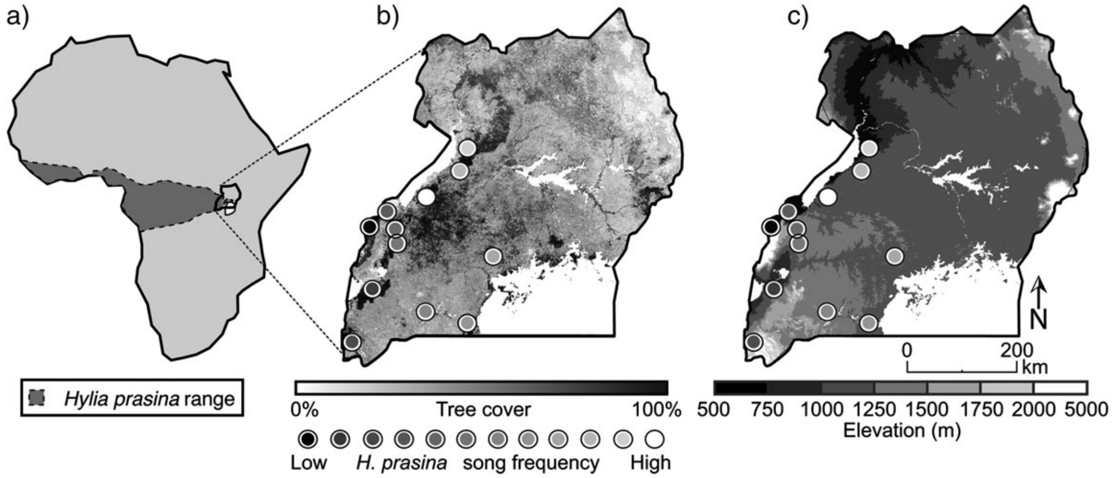

Figure 2
(a) Map of Africa illustrating the range of green hylia (*Hylia prasina*). Sites in Uganda where songs and ambient noise were recorded are overlaid on (b) a percent tree cover map and (c) an elevation map. The grayscale legend and circles illustrate the range of population means for green hylia song frequencies, with the lowest coming from Semliki National Park (3167 Hz; black) and the highest from Bugoma Forest Reserve (3328 Hz; white). These sites are little over 100 km apart. For names of sites listed in order of increasing frequency, see Table 1.

recordings at different times of day at each site. Avian vocal activity is much more prominent in the morning, so we focused specifically on the ambient noise occurring during the time of day that green hylia were most vocal. Dawn was at approximately 07:00 at most sites, and the dawn chorus was typically much louder than insect song at that time. By 09:00, insect song became very loud, largely because the majority of singing insects are ectothermic and warm up later in the morning (Jang and Gerhardt 2007). Green hylia were also most vocal in the mid morning; of the 140 green hylia recorded, 89 were recorded between 8:30 and 11:30 AM. Given a relatively equal recording effort throughout the mornings, this indicates that this time period is the preferred time for the species to sing its territorial song. Thus, to see whether green hylia song was affected by insect song, we focused on ambient noise recorded at 09:00 and 10:00. We did not include later recordings of ambient noise as insects and then typically call at much higher frequencies because of the increased temperature (Slabbekoorn 2004a, Jang and Gerhardt 2007) and go far above frequencies with a potential impact on green hylia song.

We were specifically interested in the minimum frequency of loud and continuous insect sound bands potentially masking birdsong. Therefore, we processed noise recordings from the power spectra of the five 1-s samples per recording exported from Raven 1.3 for further analysis, using the same settings and spectral resolution as for the birdsong. We measured insect sounds at the lowest frequency at which they crossed the 70 dB level in the power spectrum (Figure 3) but above the frequency of green hylia song (and hence above 3 kHz). We chose an arbitrary 70 dB threshold, which reflects a considerable amplitude peak of a loud noise band, well above average background noise levels, which were typically between 40 and 60 dB.

Absorption of sound in air can vary based on temperature and relative humidity, and the effect varies based on the frequency of the sound. We did not record temperature and relative humidity at the time of every recording and thus did not control for their effect on our ambient noise recordings. However, we tested for a possible impact on our data that could have resulted from not accounting for temperature and relative humidity using data from the 6 weather stations closest to field sites. We performed an analysis comparing noise frequencies on 26 recordings using values of absorption of sound in air in decibel per 100 m taken from tables in Harris (1967). We found that correcting for absorption of sound for temperature and relative humidity had no effect on the distribution of noise frequencies at the 70 dB threshold; indeed, the distribution was almost identical before and after such a correction ($n = 26$, $r^2 = 0.993$, $t = 58.03$, $P < 0.001$). We thus used the original values in our analyses.

Environmental variables

We predicted that broadscale climate and structural habitat variables would be important determinants of community structure of sites as well as affecting sound transmission.

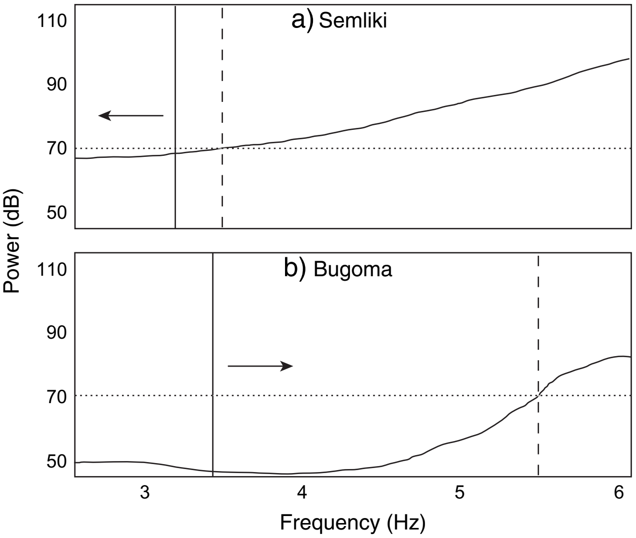

Figure 3
Power spectra illustrating background noise in examples from one 1-km^2 pixel in (a) Semliki Wildlife Reserve and (b) Bugoma Forest Reserve. Dashed and dotted lines indicate the minimum frequency of insect song at 70 dB. The solid vertical lines illustrate the mean frequencies of 2 individual green hylia recorded within those pixels. The individual at Bugoma sang at over 300 Hz higher frequencies than the individual at Semliki. Insect calling frequency crosses the 70-dB power threshold at approximately 2 kHz higher frequency in Bugoma than in Semliki. The power spectra and arrows illustrate how green hylia would be better adapted to sing at lower frequencies in Semliki and at higher frequencies in Bugoma.

Information on habitat structure was obtained from remotely sensed estimates of percent tree cover as part of the vegetation continuous field product (Hansen et al. 2002). This product is derived from passive optical measurements of the Moderate Resolution Imaging Spectroradiometer sensor mounted on NASA's TERRA and AQUA satellites. For each recording, we extracted the corresponding percent tree cover from the pixel (with 1 km spatial resolution) whose center location was nearest to the sample GPS coordinates. We also used space-born estimates of elevation from the Shuttle Radar Topography Mission (SRTM) aggregated at a 1-km^2 resolution and combined these measurements with ground-based estimates of bioclimatic variables from the WorldClim database (Hijmans et al. 2005). These bioclimatic variables capture annual mean and extremes as well as aspects of seasonality in temperature and precipitation. Annual mean temperature was strongly negatively correlated with elevation ($r = -0.953$) and was dropped from analyses to avoid multicollinearity. We elected to use elevation instead because it potentially incorporated additional relevant environmental variation missing from the annual mean temperature values.

Table 1

Localities where green hylia were recorded, with sample sizes, mean peak frequencies, and standard deviations

Locality	Sample size	Mean peak frequency (Hz)	Standard deviation
Semliki NP	10	3187.77	71.60
Queen Elizabeth NP	3	3188.33	82.53
Bwindi Impenetrable NP	9	3193.88	68.98
Semliki Wildlife Reserve	14	3193.95	27.27
Kibale NP–MUBFS	10	3199.94	74.63
Kibale NP–Kanyanchu	11	3228.24	45.54
Lake Mburo NP	5	3231.85	70.02
Mpanga Forest Reserve	7	3232.92	58.95
Sango Bay area	11	3262.75	36.66
Budongo Forest Reserve	24	3280.64	56.69
Murchison Falls NP	25	3309.66	61.66
Bugoma Forest Reserve	7	3327.72	49.21

Localities are listed in order of increasing mean peak frequency. NP = National Park.

Data analysis

We used path analysis (Wright 1921) to test our hypotheses of the direct effects of the environment on bird and insect sound frequency, the direct effects of insect sounds on birdsong, and the indirect effects of the environment on birdsong via its effect on insect sounds. Although similar to multiple regression, where predictor variables are all exogenous, path analysis can be used to calculate direct and indirect effects when endogenous predictor variables are included. These endogenous predictors might be influenced by exogenous variables and may themselves influence the response variables (Wright 1934, Cohen J and Cohen P 1983). We used maximum likelihood estimation in our path analysis model, but for comparison, we also performed a similar test using ordinary least squares (OLS) in a multiple regression framework by following the Baron and Kenny (1986) method. The Baron and Kenny method requires a 3-step approach performing multiple regression on the response variable using just the exogenous variables as predictors (elevation, percent tree cover, and annual precipitation), then not only the same test but also including the mediator variable (insect sound frequency) as a predictor, and finally a multiple regression on the mediator as the response variable with the 3 exogenous predictors. In order to determine the significance of indirect effects following the Baron and Kenny method, we used the Sobel (1982) test. We could not use every individual insect sound recording in the analyses because they were collected independently of the green hylia recording locations. We therefore used data for the environment and insect sounds collated at the 1-km^2 pixel level for each 1-km^2 pixel within which green hylia were recorded. The environmental and insect sound data were nested in the path analysis by robust standard error estimation (Williams 2000), which adjusts for serial correlation that could occur within clusters (here 1-km^2 pixels). Our analyses focused on 55 individuals for which we had matching insect sound data nested within twenty 1-km^2 pixels. Path analysis with standardized coefficients was performed using Mplus 5.1 (Muthén LK and Muthén BO 2008).

RESULTS

Green hylia song frequency showed much variation between populations (Table 1), with individual mean frequencies ranging between 3082 and 3456 Hz (mean = 3248 ± 72 Hz). The minimum frequencies of insect sounds were positively correlated with green hylia song frequencies after accounting for the effects of elevation, tree cover, precipitation, and within-pixel variation ($n = 55$, $P = 0.01$; Figure 4). This is consistent with the hypothesis that green hylia need to sing at lower frequencies in order to avoid masking when insect sounds are relatively low in frequency. Green hylia song frequencies were also significantly lower at higher elevations ($P = 0.005$) and at lower percent tree cover ($P = 0.001$). Minimum insect sound frequency (at 70 dB) was similarly affected, with lower frequencies at higher elevations ($P = 0.004$) and lower tree cover levels ($P < 0.001$). Annual precipitation had no direct effect on either green hylia song ($P = 0.876$) or insect song frequencies ($P = 0.166$). Overall, insect song and the environmental variables explained a significant amount of green hylia song frequency variation ($r^2 = 0.431$, $P < 0.001$) with the environment variables also explaining significant variation in insect song frequency ($r^2 = 0.474$, $P = 0.004$). Using the Baron and Kenny method, results are essentially the same: except that because of the different estimation method (OLS) and the multistep approach, effects, and P values are slightly different. The direct effects on peak song frequency using multiple regression were insect sound: $t = 2.32$, $P = 0.031$;

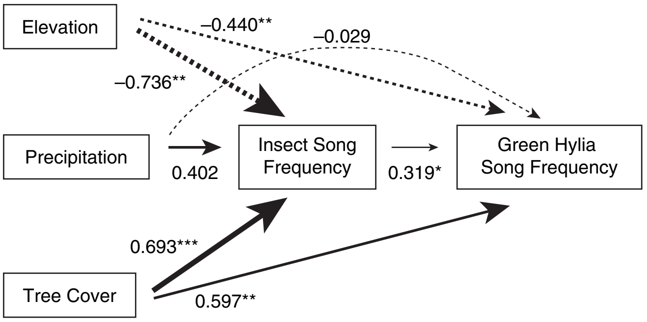

Figure 4

Path diagram illustrating both the direct effects of the environment and insect song on green hylia song and the indirect effects of the environment on green hylia song via their influence on insect song. Standardized path coefficients are given alongside each path. Arrow thickness illustrates effect size, solid lines indicate positive effect on song frequency, and dashed lines indicate negative effect. $*P < 0.05$, $**P < 0.01$, and $***P < 0.001$.

elevation: $t = -2.48$, $P = 0.023$; tree cover: $t = 2.92$, $P = 0.009$; and precipitation: $t = -0.15$, $P = 0.884$. Effects on insect sound were as follows: elevation: $t = -2.61$, $P = 0.017$; tree cover: $t = 4.06$, $P < 0.001$; and precipitation: $t = 1.21$, $P = 0.242$.

In addition to the direct effects of the environment on green hylia song, there were also indirect effects based on the effects of climate and habitat via their effects on insect song frequencies. Both elevation and tree cover had significant indirect effects on green hylia song via their effect on insect sound (elevation: $P = 0.011$; tree cover: $P = 0.027$) so the total effect (direct and indirect) of each on green hylia song was even stronger (elevation: $P < 0.001$; tree cover: $P < 0.001$). Annual precipitation had no indirect effect or total effect on green hylia song frequency (indirect: $P = 0.158$; total: $P = 0.656$). Because of the different estimation approach and the separate steps used in the Baron and Kenny multiple regression approach, the raw coefficients and standard errors are a little different and significance testing may yield slightly different results: for the indirect effect (via insect sound) of elevation on song frequency: $t = -1.95$, $P = 0.051$; tree cover on song frequency: $t = 2.02$, $P = 0.043$; and annual precipitation on song frequency: $t = 0.41$, $P = 0.68$. The indirect effects of tree cover and elevation on song frequency are in the same direction as their direct effects on song frequency, implying the overall effect of those environmental factors on song has increased.

DISCUSSION

We found considerable variation in song frequencies among different populations of green hylia. The peak frequencies of the simple 2-note song correlated significantly with elevation, tree cover, and frequency peaks of potentially masking insect sounds. Green hylia males sang at lower frequency at higher elevation and at lower tree cover levels. These environmental variables affected song frequencies not only directly but also indirectly through their effect on noise spectra caused by the calling insect communities. Lower frequencies in loud insect sound bands were correlated with lower frequencies in green hylia song.

Green hylia sing narrow bandwidth songs and must sing in relative frequency troughs of ambient noise to escape masking. Birds that sing broad- bandwidth songs can still transmit portions of their signal when continuous bands of insect sound are present, but birds with narrow bandwidth songs must shift their frequency to transmit their messages to their intended receivers. Such frequency shifts could be widespread in tropical forest birds. With the considerable acoustic competition present in tropical forests, narrowband singers, like green hylia, may need to adapt their songs to frequencies where propagation is effective. Variation in song frequencies because of variation in masking background noise may thus be commonplace.

Insect sound frequency varied significantly between populations. One possible explanation for this variation is that different singing insect assemblages exist between sites. A study on cicadas across habitats in Southern Africa found that forest dwelling cicadas were generally larger than those found in open habitats, and the vast majority of larger cicadas were endothermic (Sanborn et al. 2003). Larger endothermic cicadas can sing in colder areas and early in the morning. Thus, based on the negative correlation between song frequency and body size found in cicadas (Bennet-Clark and Young 1994), we expect it is these larger cicadas that sing at lower frequencies. The smaller ectothermic cicadas can only start singing when conditions are warmer, and we suspect that the high-frequency sounds are produced by these smaller species.

Our results also demonstrate that there are consistent patterns of insect sound frequency as well as green hylia song frequency with elevation. Elevation is strongly negatively correlated with temperature, which has previously been found to influence insect song (Sanborn et al. 2003; Jang and Gerhardt 2007). Typically, temperature levels will be higher at lower elevations, allowing crickets, katydids, and other thermoconformers to stridulate faster and create higher frequency song (reviewed in Sanborn 2006). These patterns will also be reflected within sites where temperature levels increase through the morning (Slabbekoorn 2004a). The present results show that green hylia song is affected not only indirectly by elevation via its effect on insect sound but also directly. Green hylia may follow Bergmann's rule, with larger individuals occurring in colder areas such as at high altitude (Ashton 2002; Kirschel et al. 2009). A negative correlation between birdsong frequency and elevation may thus be expected because larger birds have a tendency to sing at lower frequencies (Ryan and Brenowitz 1985; Podos et al. 2004). Although we did not measure body size specifically for this study, there is some evidence for a link between body size and song frequency in green hylia. Songs recorded further west in Cameroon are much higher in frequency (3788 ± 64 Hz, $n = 24$, Slabbekoorn et al. 2002) than those recorded in Uganda for this study (3248 ± 72 Hz, $n = 140$). Although we do not have a direct morphological comparison from the same sites, Urban et al. (1997) showed that green hylia are considerably larger in Uganda (males 14.1 g [range 10–16.5 g], $n = 48$; females 12.1 g [range 10–15 g], $n = 30$) than they are further west in Liberia (males 12.7 ± 1.4 g, $n = 10$; females 10.5 ± 1.3 g, $n = 11$), which is consistent with larger birds singing lower frequency songs further east. A pattern of increasing body size and lower frequency song at increasing elevations would be consistent with findings in another African forest bird (Kirschel et al. 2009).

Interestingly, we found that song frequencies were higher at sites with greater percent tree cover, in contrast to some previous studies (e.g., Morton 1975; Wiley 1991). However, for this study, lower percent tree cover is indicative of secondary forest, which has a denser midstory than found in primary forest (Carswell et al. 2005). Singing lower frequency songs may thus have resulted from attenuation of higher frequencies in the denser midstory of secondary forest.

Previous studies that have shown that birdsong varies according to environmental transmission properties and ambient noise (Morton 1975; Wiley and Richards 1982; Ryan and Brenowitz 1985; Slabbekoorn and Smith 2002b), typically dichotomized habitat into open and closed forest, comparing song features such as frequency and rate (e.g., Morton 1975; Wiley 1991). Dichotomizing sites into habitat types can be a subjective process and by doing so, some of the direct relationships between certain environmental features and variation among populations can be obscured. We tested the effects of elevation, tree cover, and precipitation using data at the 1-km^2 pixel level, thus providing a more direct understanding of how these environmental variables may influence acoustic communication in both insects and birds. By using path analysis, we were able to differentiate between direct and indirect effects of elevation, tree cover, and precipitation on green hylia song. The path analysis has thus allowed us to reveal the intriguing acoustic interrelationships of birds and insects within tropical communities, and how the environment can affect each in turn. We thus believe that path analysis can aid in better understanding how animals respond to biotic and abiotic factors in an ecologically complex tropical forest community.

Green hylia song variation among populations may have a genetic basis, may be a result of behavioral plasticity, or may be influenced by a combination of these factors (Brumm and

Slabbekoorn 2005; Patricelli and Blickley 2006), though additional data pertaining to these mechanisms would be required to determine their role. The impact of behavioral plasticity on song variation among individuals may emerge at an ontogenetic or immediate temporal scale. Auditory feedback under local noise conditions may steer song development in such a way that birds crystallize those songs that they hear best against the background noise (Slabbekoorn and den Boer-Visser 2006). Auditory feedback could also drive immediate spectral flexibility in response to changing noise levels, as reported for Bengalese finches (*Lonchura striata*) in response to experimental masking of specific song elements in a laboratory study (Tumer and Brainard 2007). An impact of learning or behavioral plasticity does not exclude underlying genetic variation for acoustic variation at the population level (Slabbekoorn and Smith 2002a; Price et al. 2003) and may in fact promote differentiation and speciation under certain conditions (Ellers and Slabbekoorn 2003; Lachlan and Servedio 2004).

In conclusion, we have shown how specific climate and habitat features affect the sounds of tropical forests. The environment can influence species distributions and their behavior and thereby affect noise profiles generated by the local sound-generating community. Using path analysis, we were able to tease apart direct and indirect effects of the environment on birdsong. Our case study on green hylia shows how a narrowband specialist, with high potential for being masked, can be tuned to geographic variation in habitat-dependent noise profiles. These data confirm the role of the environment in shaping geographic variation in birdsong and provide further insight into how acoustic signals important to species recognition may diverge and subsequently play a role in ecological speciation (Slabbekoorn and Smith 2002a).

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