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Phylogenetic and ecological determinants of the neotropical dawn chorus

Karl S. Berg[1,*], Robb T. Brumfield[2] and Victor Apanius[1,†]

[1]*Department of Biological Sciences, Florida International University, Miami, FL 33199, USA*
[2]*Museum of Natural Science, 119 Foster Hall, Louisiana State University, Baton Rouge, LA 70803, USA*

The concentration of avian song at first light (i.e. the dawn chorus) is widely appreciated, but has an enigmatic functional significance. One widely accepted explanation is that birds are active at dawn, but light levels are not yet adequate for foraging. In forest communities, the onset to singing should thus be predictable from the species' foraging strata, which is ultimately related to ambient light level. To test this, we collected data from a tropical forest of Ecuador involving 57 species from 27 families of birds. Time of first song was a repeatable, species-specific trait, and the majority of resident birds, including non-passerines, sang in the dawn chorus. For passerine birds, foraging height was the best predictor of time of first song, with canopy birds singing earlier than birds foraging closer to the forest floor. A weak and opposite result was observed for non-passerines. For passerine birds, eye size also predicted time of first song, with larger eyed birds singing earlier, after controlling for body mass, taxonomic group and foraging height. This is the first comparative study of the dawn chorus in the Neotropics, and it provides the first evidence for foraging strata as the primary determinant of scheduling participation in the dawn chorus of birds.

Keywords: song; dawn chorus; foraging strata; tropical forest

1. INTRODUCTION

The reason birds sing so emphatically at dawn has several non-mutually exclusive explanations. The acoustic transmission hypothesis is based on the fact that atmospheric conditions in the morning are more favourable for song propagation in terms of transmission distance (Henwood & Fabrick 1979; Brenowitz 1982) and signal fidelity (Brown & Handford 2003). Birds may also sing at dawn because they have excess energy reserves that might have been used to survive variable night-time environmental conditions. This energy storage stochasticity hypothesis predicts that the participants in the dawn chorus follow state-dependent decision rules based on their energy reserves at these times of day (Hutchinson 2002). The inefficient foraging hypothesis states that the timing of dawn song is related to light availability. Birds become active at twilight when light levels are insufficient for foraging, yet adequate for social communication as well as predator avoidance. As evidence, Kacelnick (1979) showed that foraging becomes profitable in captive Great Tits (*Parus major*) at light levels when dawn singing in this species typically ends. Thus, the curtailment of dawn singing appears to be linked to the start of the day's foraging activity.

A puzzling aspect of the dawn chorus is why individual temperate songbird species begin singing at characteristic times each morning (Allen 1913). Acoustic transmission would be favourable for all species at dawn and an experimental test of this hypothesis did not show interspecific distinctions (Brown & Handford 2003). State-dependent hypotheses concern individual participation rates and so do not directly address the species-specific sequential participation unless body mass, which is related to fasting resistance, is related to the probability of singing at dawn (Hutchinson 2002). The inefficient foraging hypothesis (Kacelnick & Krebs 1982) was supported by phylogenetically independent regression of (mass-adjusted) eye size on time of first song (Thomas *et al.* 2002). Species with relatively large eye sizes, which presumably initiate foraging under lower light levels, sang earlier in the dawn chorus; body mass by itself had little predictive power. Although multiple selective factors may favour vocal communication at twilight, eye size appears to predict the species-specific sequence of singing in temperate songbird communities, suggesting that ambient light level determines the initiation of daily vocal communication.

Our understanding of the dawn chorus is based largely on temperate zone studies of the oscine radiation of passerine birds (Allard 1930; Leopold & Eynon 1961; Thomas *et al.* 2002). Less is known about the dawn chorus in the tropics (Kroodsma *et al.* 1996; Staicer *et al.* 1996), which includes a substantial number of suboscine and non-passerine taxa with greater diversity of morphology and foraging modes. For the inefficient foraging hypothesis to be a general explanation, the species-specific singing times should be predictable regardless of whether light is attenuated at twilight or along ecological gradients

* Author and address for correspondence: Department of Environmental Science, Policy & Management, University of California, 137 Hilgard Hall No. 3114, Berkeley, CA 94720-3114, USA (kberg@nature.berkeley.edu).
† Present address: Department of Biology, Wake Forest University, PO Box 7325, Winston-Salem, NC 27109, USA.

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(e.g. vegetation density, vertical stratification, distance from edge). In broad-leaf, tropical forests light intensity attenuates by up to two orders of magnitude between the top of the canopy and the understory (Lee 1987; Engelbrecht & Herz 2001). In general, canopy foraging species should sing earlier than ground foraging species. The relationship between eye size and foraging strata is more difficult to predict. In dense forest habitats, eye size would be expected to vary inversely with foraging height, as eye size evolves to match the foraging microenvironment.

Despite light attenuation by vegetation, visual sensitivity of individual species may compensate so that time of first song is independent of foraging height. On the other hand, eye size may be evolutionarily conserved and unrelated to foraging height if speciation events involved rapid shifts in foraging strata. In this case, foraging height would be the primary determinant of the onset of song and eye size may play a secondary role. To address this issue, we measured open-field light level, time of first song, foraging height and eye size in a phylogenetically diverse avian community in a tropical forest of lowland Ecuador.

2. MATERIAL AND METHODS

(a) *Time of first song*

The study was conducted at a 1000 ha forest block 5 km east of the town of Don Juan, in the province of Manabi, Ecuador (80°12′ W, 0°11′ S). The rolling topography was covered with moist and humid tropical forest. Canopy height ranged between 20 and 25 m. The dawn chorus was recorded at six evenly spaced (greater than 200 m apart) mature forest sites. At each site, recordings were made on three to five mornings between 21 January and 27 February 2003, with sampling dates evenly spaced across the study period. This sampling period coincided with the wet season and the breeding season for many bird species in western Ecuador (Marchant 1959).

Recordings were made with an MKH20 omni-directional microphone (Sennheiser Electronic Corp., Wedemark, Germany) mounted 1.5 m above ground, a TC-D5 Pro II recorder (Sony Corp., Tokyo, Japan) and Type II SM cassette tape (TDK Electronics Corp., Garden City, New York, USA). Recordings were synchronized at the beginning of nautical twilight each day (i.e. when the sun was 12° beneath the horizon), and continued for 100 min. Nautical twilight was determined using the Astronomical Applications website of the US Naval Observatory (http://aa.usno.navy.mil).

Analogue recordings were digitized and sonograms/recordings scored for the time of first vocalization (± 1 min) for each species. The time of first song was measured as the number of minutes between the beginning of nautical twilight and the first recorded song for that species. For 57 of the 75 species that sang in the dawn chorus, we recorded the time of first song on multiple mornings (electronic supplementary material) and found this trait to be repeatable when pooled across six sites (intraclass correlation coefficient $r_i = 0.54$, $F_{56,648} = 15.26$, $p < 0.0001$). Neither site nor date affected singing times for a subset of 18 species that sang on multiple mornings at all sites ($r^2_{site} = 0.0186$, $F_{5,363} = 1.37$, $p = 0.23$; date: $r^2_{date} = 0.0000$, $F_{1,367} = 0.0$, $p = 0.99$). Based on this result, we pooled observations across sites and dates and used the mean time of first song for the 57 species.

Irradiance between 400 and 700 nm was measured ($\pm 5\%$) every minute during dawn recordings using two LI-190S quantum sensors with a sensitivity of approximately 0.001 $\mu mol\, s^{-1}\, m^{-2}$ and a LI-1400 data logger (Licor, Lincoln, Nebraska, USA). Means were calculated from the two sensors in order to reduce calibration error. The sensors were located in a clearing 25 m from forest edge on a level plane 3 m above the ground.

(b) *Ecomorphology*

Foraging height of birds was estimated following Remsen & Robinson (1990). Flagging tape placed on tree limbs at 5, 10 and 15 m above the ground was used as a reference frame. Vertical position of birds (within 1 m) was estimated between 08.00 and 10.00 h. Foraging height was repeatable ($r_i = 0.67$, $F_{36,158} = 11.74$, $p < 0.0001$), and it is considered to be a species-specific trait in tropical forest birds (Pearson 1971; Bell 1982; Walther 2002). Although distance beneath the canopy may be a more relevant metric, our measurements provide a reasonable approximation of ambient light across foraging strata, given the generally uniform canopy height at the study site.

Transverse eye diameter (based on eyes removed from wet preserved specimens) and body mass were obtained from Ritland (1982). Additional eye diameter data were obtained following Thomas *et al.* (2002) and taken from study skins housed in the collections of the Louisiana State University Museum of Zoology and the Academy of Natural Sciences of Philadelphia. Length of eye was measured as the distance between the anterior end and the hindmost point of the eye opening (Baldwin *et al.* 1931). Since the globe of the eye is partially concealed by the orbit and there exists potential for shrinkage in preserved skins, measurements from Ritland (1982) were larger than those from skins. Thus, measurements from museum skins (Y) were standardized with the wet-preserved specimens (X) for eight species by increasing eye size by a factor equal to the slope of the regression for 17 species common to both datasets ($Y = 0.82$ (± 0.63 s.e.) + 1.54 (± 0.080 s.e.) X; $r^2 = 0.96$, $F_{1,15} = 368.42$, $p < 0.0001$). Eye diameter and body mass measurements were highly repeatable within species (eye: $r_i = 0.89$, $F_{32,65} = 25.60$, $p < 0.0001$; body: $r_i = 0.98$, $F_{31,64} = 183.03$, $p < 0.0001$). Log-transformed eye diameter correlated with log(body mass) across all species ($r = 0.77$, $p < 0.0001$, $n = 42$).

(c) *Comparative analyses*

We grouped species singing in the dawn chorus into three deeply rooted and unambiguous avian clades: non-passerines, suboscine passerines and oscine passerines (figure 1), and used one-way ANOVA to determine whether traits differed as a function of ancestry based on these broad taxonomic groups. Individuals of closely related species may sing at particular times because of a common ancestral trait and not as a result of morphology or behaviour of extant birds, which could overestimate degrees of freedom in comparative analyses. To assure independence of observations, we employed Felsenstein's method (1985) of calculating phylogenetic independent contrasts in character traits. We created a phylogenetic hypothesis based on Sibley & Ahlquist (1990), but incorporated two recent discrepancies: *Sclerurus* was considered basal to ovenbird (Furnariidae) and woodcreeper (Dendrocolaptidae) sister groups (Irestedt *et al.* 2002; Chesser 2004); and *Manacus* was placed basal to flycatchers (Tyrannidae) (Johansson *et al.* 2002). For missing species, we assumed sister clades based on Ridgely & Greenfield (2001) and Birdsley (2002). Incorporating these changes into Sibley & Ahlquist's phylogeny precluded

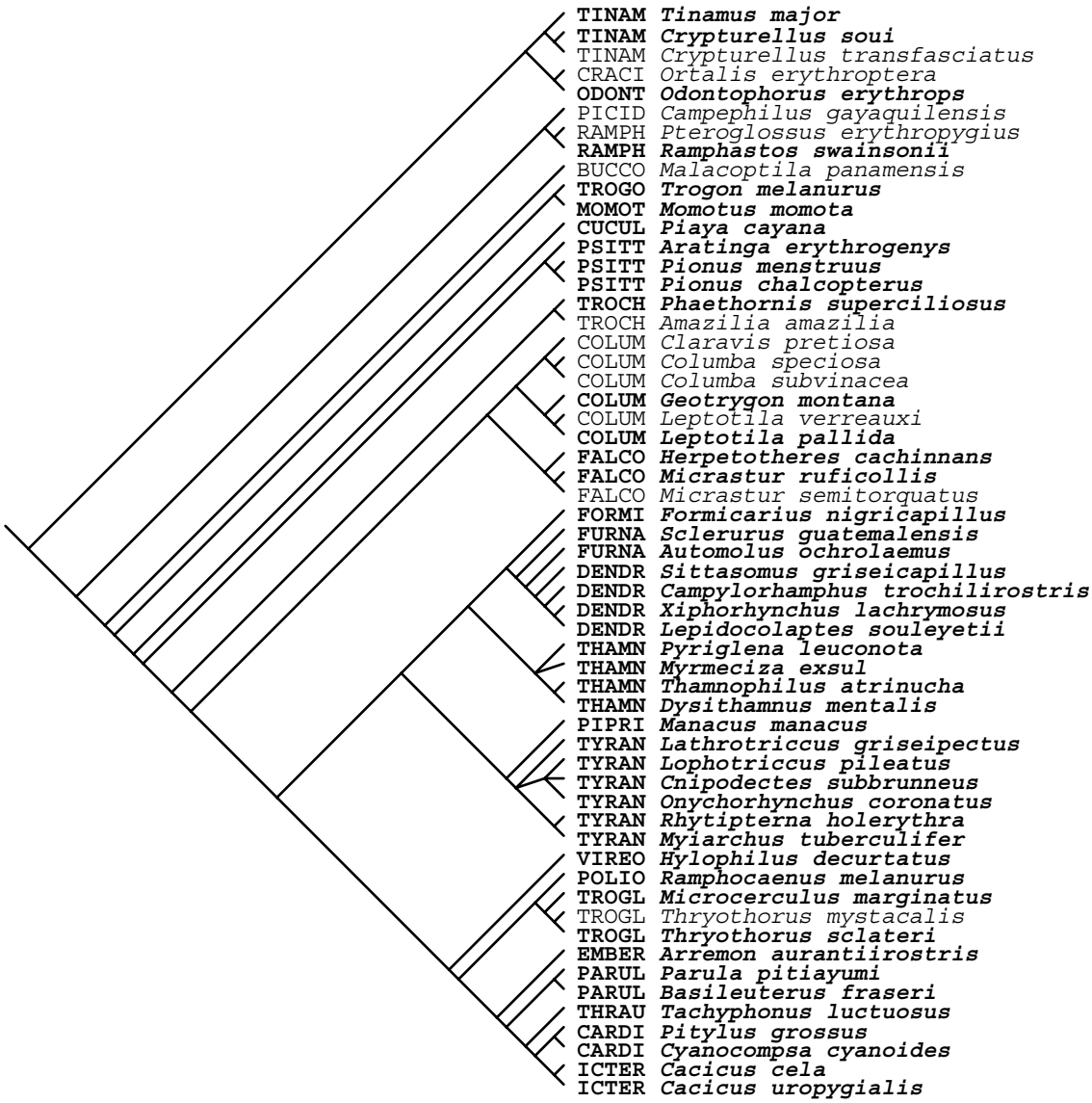

Figure 1. Phylogenetic hypothesis for the 57 species that sang in the dawn chorus at a moist tropical forest, Manabi Province, Ecuador on multiple mornings during a 25 morning sample period. The 45 species names in bold were used in the analysis of phylogenetic independent contrasts. Five letter uppercase abbreviations refer to the taxonomic family names shown in electronic supplementary material.

analyses using variable branch lengths. Phylogenetic independent contrasts were calculated using CAIC, v. 2 software (Purvis & Rambaut 1995). Analyses that assumed random walk (Grafen's branch lengths) and punctuated (equal branch lengths) models of trait evolution were conducted and compared. Because the results did not vary significantly, we follow Russo *et al.* (2003) and report only results assuming equal branch length using the phylogenetic hypothesis in figure 1.

(d) *Statistical analyses*

All statistical analyses were performed using SAS (v. 9.1, Cary, North Carolina, USA). Repeatability (intraclass correlation coefficient) of measurements was calculated from variance components (NESTED Procedure). Correlation coefficients were calculated using the CORR procedure. General linear models (GLM Procedure) were used for ANOVA and ANCOVA. The time of first song was based on a variable number of measurements on different days/locations with the number of observations used in weighted least squares GLM. Residuals were examined for evidence of heteroscedasticity and non-normality; log-transformations were employed as indicated. Phylogenetic independent contrasts were analysed with regression lines (REG procedure) forced through the origin. Our results satisfied the model assumptions outlined by Purvis & Rambaut (1995).

3. RESULTS

(a) *The neotropical dawn chorus*

Representatives of all 11 avian orders known to be present in the study area sang in the dawn chorus. Representatives of 82% of the non-passeriform and all of the suboscine and oscine passerine families participated in the dawn chorus (electronic supplementary material). Of the 118 resident bird species documented at the study site, 51% of the non-passerine, 63% of the suboscine passerine and 67% of the oscine passerine species were recorded in the dawn chorus. The probability that a particular species sang in the dawn chorus was not related to its taxonomic affiliation, i.e. family, order or classification as non-passerine, suboscine or oscine clade (all $p > 0.33$).

Therefore, the neotropical dawn chorus included vocalizations across the taxonomic spectrum of resident bird species (figure 1).

Suboscine passerine species sang their first song significantly earlier than oscine passerines, while the time of first song was intermediate for non-passerine species (table 1). The (log-transformed) number of minutes after nautical twilight was strongly correlated with the (log-transformed) open-field irradiance on each morning sampled ($r^2=0.967$–0.981, $n=116$–121). However, the variance component for date was not significant (0.025, −0.004–0.055 95% CI), indicating that light levels were not consistently different among sampling dates. The strong correlation between time and light at twilight and the limited variation in open-field irradiance between dates precluded a direct analysis of ambient light level in relation to the first vocalization of each species. Nonetheless, the species-specific time of first song accurately reflected the ambient light level unobstructed by vegetation.

(b) *Time of first song and foraging height*

Foraging height did not vary between taxonomic groups (table 1). Time of first song was not directly related to foraging height ($F_{1,41}=1.02$, $p=0.32$), but was related to the foraging height × taxonomic group interaction ($F_{5,37}=9.38$, $p<0.0001$). Non-passerine species showed a positive relationship between foraging height and time of first song ($r_s=0.54$, $n=16$, $p=0.032$; figure 2), which depended on the early singing of five ground-dwelling taxa. Excluding these species, there was no significant relationship between foraging height and time of first song for non-passerine birds ($r_s=-0.03$, $n=11$, $p=0.93$). In contrast, passerine species showed a highly significant negative relationship ($F_{1,24}=36.59$, $p<0.0001$, $r^2=0.61$) when controlling for the time difference between suboscine and oscine groups (figure 2). On average, passerines that foraged in the top of the canopy sang 44.4±5.2 min earlier than ground foragers.

(c) *Time of song, foraging height and eye size*

Non-passerine species that sang in the dawn chorus had greater body masses and eye sizes than passerine species (table 1). We used body mass as a covariate and refer to mass-adjusted eye size as relative eye size. Among passerines, foraging height was not related to body mass ($F_{1,23}=0.21$, $p=0.65$) or relative eye size ($F_{1,23}=1.41$, $p=0.25$). Time of first song was not related to relative eye size ($F_{1,23}=1.20$, $p=0.33$), controlling for passerine clade. Time of first song was significantly and negatively related to relative eye size when foraging height was included in the model for passerine birds (table 2). Body mass and eye size were highly correlated across all birds (see §2), which could produce biased parameter estimates (Freckleton 2002). However, almost identical results were obtained using the residuals of a reduced major axis regression of body mass on eye size. Thus, passerine species with large eyes, relative to their body size, sang earlier in the dawn chorus, but only after accounting for their foraging strata.

(d) *Phylogenetic independent contrasts*

Pooling all taxa, contrasts in the time of first song were not related to contrasts in foraging height, body mass or

Table 1. Mean±standard errors and the number of species (n) of the parameters as a function of taxonomic group. (Significant differences between groups have different superscript letters.)

time of first song (min): ($F_{2,54}=3.98$, $p=0.024$, $r^2=0.13$)	
non-passerine[ab]	59.14±4.40 (27)
suboscine[a]	46.18±4.51 (17)
oscine[b]	62.49±4.41 (13)
log(foraging height) (m): ($F_{2,40}=0.37$, $p=0.69$, $r^2=0.02$)	
non-passerine	0.75±0.14 (15)
suboscine	0.70±0.09 (18)
oscine	0.86±0.17 (10)
log(body mass) (g): ($F_{2,40}=16.66$, $p<0.0001$, $r^2=0.45$)	
non-passerine[a]	2.15±0.15 (15)
suboscine[b]	1.39±0.06 (18)
oscine[b]	1.37±0.11 (10)
log(eye size) (mm): ($F_{2,39}=20.34$, $p<0.0001$, $r^2=0.51$)	
non-passerine[a]	1.18±0.04 (15)
suboscine[b]	0.96±0.02 (18)
oscine[b]	0.94±0.04 (9)

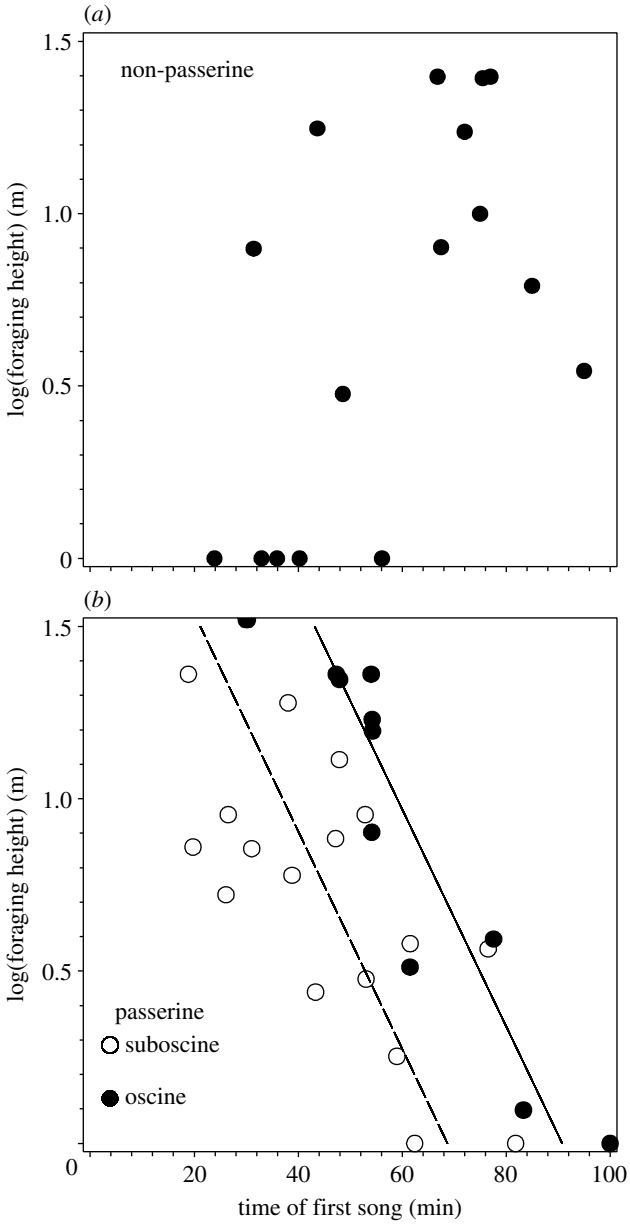

Figure 2. Time of first song as a function of foraging height for (*a*) non-passerine and (*b*) passerine species.

Table 2. ANCOVA of time of first song as a function of passerine clade (suboscine or oscine), foraging height, body mass and eye size. (Model $F_{5,20}=12.14$, $p=0.0001$, $r^2=0.71$.)

parameter	estimate ± s.e.	p
intercept (suboscine)	120.1 ± 25.3	0.0001
oscine	18.9 ± 5.2	0.0017
log(foraging height)	−38.7 ± 6.0	<0.0001
log(body mass)	20.4 ± 10.2	0.06
log(eye diameter)	−75.4 ± 31.0	0.025

relative eye size ($p>0.48$). Contrasts in eye size were correlated with contrasts in body mass (all $r=0.66$, $p=0.0001$, $n=35$), but neither were correlated with contrasts in foraging height (all $p>0.95$).

When we restricted the analysis to passerine taxa, contrasts in time of first song were significantly related to contrasts in foraging height and eye size, using the body mass contrasts to control for body size as in previous analyses (table 3). Body mass contrasts were correlated to eye size contrasts ($r=0.77$, $p=0.0001$, $n=20$). Contrasts in time of first song were not related to contrasts in body mass and eye size ($p>0.41$), nor were foraging height contrasts related to body mass and eye size contrasts ($p>0.35$). These results reinforce our previous conclusion that foraging strata and, secondarily, relative eye size predict the time of first song for passerines, but not necessarily for all birds participating in the dawn chorus.

4. DISCUSSION

This is the first comparative study of the dawn chorus in the Neotropics and the first to include a substantial number of suboscine and non-passerine species. This enabled a comparison of the ability of phylogenetic and ecomorphological factors to predict the timing of dawn song. We demonstrated that the time of first song is a species-specific trait across 57 species representing 27 families and eight orders. We showed that the neotropical dawn chorus is not disproportionately represented by species from the songbird order Passeriformes. However, the functional equivalence of dawn singing in passerine and non-passerine species is open to question.

For the passerine lineage, the species-specific time of first song was primarily (and inversely) related to foraging height and was secondarily (and also inversely) related to relative eye size. Therefore, the onset of the dawn chorus depended on ambient light level, as it is attenuated through the vegetation column and on visual sensitivity as inferred from mass-corrected eye size. That eye size was significant after controlling for foraging height indicated that eye sizes were estimated with adequate precision after correction of shrinkage in museum specimens. This combination of results supports the inefficient foraging hypothesis by showing the primacy of light in predicting the sequence of participation in the dawn chorus.

Among non-passerine species, the time of first song was not predictable from foraging height or relative eye size. This discrepancy may be due to the diversity of diets and foraging modes within the non-passerine clades. For example, non-passerine birds that feed on conspicuous fruits may have lower ambient light requirements than

Table 3. Regression analysis of phylogenetic independent contrasts in the time of first song as a function of foraging height, body mass and eye diameter in passerines. (Model $F_{3,17}=10.63$, $p=0.0004$, $r^2=0.65$.)

parameter	estimate ± s.e.	p	r^2
foraging height contrast	−34.93 ± 6.73	0.0001	0.50
body mass contrast	35.51 ± 13.60	0.018	0.02
eye diameter contrast	−87.08 ± 34.54	0.022	0.13

passerine species that glean for cryptic insects. We attempted to include these predictive factors, but our results were inconclusive. Our impression is that diet and foraging methods varied considerably among the species-poor non-passerine lineages in contrast to the largely insectivorous and species-rich passerine branch. Furthermore, diet, foraging mode and relative eye size are likely to coevolve with increased eye size being favoured by pursuit hunting (to increase acuity) as well as nocturnality (to increase sensitivity; Garamszegi *et al.* 2002). This may underlie our success in identifying strong relationships between the time of dawn song and ecomorphological factors in passerines. Since the inefficient-foraging hypothesis is premised on foraging profitability, future research needs to account for diet and foraging modes in order to expand its generality to non-passerine taxa.

Surprisingly, eye size and foraging strata did not covary. However, this is compatible with the hypothesis that eye size is evolutionarily conserved (Ritland 1982). Eye size was an indirect predictor of the time of first song, suggesting that both eye size and foraging strata are independent evolutionary responses to light availability. Because the proximate ecological conditions better predicted the time of first song, we speculate that foraging strata and the timing of dawn song are evolutionarily labile.

Unlike studies of the dawn chorus in temperate regions, the community we studied was well represented by the suboscine passerine lineage. We were surprised that oscine species sang later than suboscine species, although they did not differ in foraging height, body mass or relative eye size. Leopold & Eynon (1961) suggested that phylogenetic differences in the avian retina might help explain the differential start of dawn song. Our results point to the possibility of differential retinal sensitivity between sub- and oscine clades of passerine birds.

Our results are also consistent with the acoustic transmission hypothesis to the extent that increasing ambient light levels at dawn are associated with degradation of transmission properties via atmospheric turbulence. Disruption of signal transmission might also proceed from the canopy toward the forest floor so that canopy species should sing earlier than floor dwelling species. However, monotonically increasing light levels combined with the explanatory role of eye size further support the primacy of ambient light for determining the species' sequence in the dawn chorus, but do not negate that light may function as a *zeitgeber* for deteriorating transmission conditions. Distinguishing between inefficient foraging and acoustic transmission hypotheses may also require a better understanding of the relationship between foraging and singing strata. We measured foraging height because of its relevance to the inefficient

foraging hypothesis and because measurement of singing height in dim-lit forests is more difficult, but may have been relevant for the acoustic transmission hypothesis.

The transition between dawn singing and foraging activity is perhaps more relevant to the inefficient foraging hypothesis (Thomas *et al.* 2002), but is more problematic to measure, in part because many avian species continue vocalizing, albeit at reduced rates, throughout the day. Most studies of the dawn chorus have focused on the time of first song, because it can be unambiguously measured. We are currently analysing the temporal distribution of song output at dawn and have observed three basic patterns: (i) an abrupt cessation; (ii) gradual reduction; and (iii) no change (K. S. Berg 2005, unpublished observation). Whether the intensity of vocal output at dawn is predictably associated with these three patterns is unknown.

The temporal sequence to song onset begs an additional question: why not sing earlier? Singing earlier would be advantageous according to the acoustic transmission hypothesis in that conditions are favourable and that masking of acoustic signals by other species could be avoided. An earlier onset to song would not adversely affect foraging time, but like foraging it is constrained by light availability. The previous explanations imply only indirect costs (i.e. not singing, not foraging), while selection on animal signals is likely greatest when significant costs are involved (Endler 1992). Our results corroborate the hypothesis that visual detection of approaching predators directly regulates the onset to the dawn chorus (Thomas *et al.* 2002), and is also predictable from ambient light levels. In this model, birds begin to sing when ambient light levels are sufficient to discriminate predators that use vocal cues to locate their prey (Krams 2001). As ambient light levels increase to allow profitable foraging, birds switch from primarily singing to foraging. In this way, sufficient illumination to minimize predation risk will be the primary determinant of the start of dawn singing, while illumination level at a particular foraging stratum will determine the decline in song output. Eye size will be a relevant predictor for both transition times in this model, as it relates to both visual acuity and sensitivity.

Further resolution of the selective factors underlying the dawn chorus requires integrating: (i) predation risk; (ii) diet and foraging mode; (iii) singing height and the onset to foraging; (iv) acoustic transmission properties; and (v) spectral differences in ambient light and how this information is processed by the avian retina. We have not addressed, but recognize, the critical role of vegetation and the structure of acoustic signals for effective transmission. Our study has shown how animal communication is influenced by visibility in forests and how these two sensory domains are integrated in birds.

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