

Dawn chorus variation in East-Asian tropical montane forest birds and its ecological and morphological correlates

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Abstract

Many birds in breeding seasons engage in vigorous dawn singing that often turns to a prominent chorus. We examined dawn chorus variation of avian assemblages in a tropical montane forest in Taiwan and tested the hypothesis that onset sequence is affected by eye sizes, foraging heights, and diet of birds. Chorus onset and duration varied between sampling months, but generally peaked in the prime breeding season. Overall dawn chorus length increased with, but mean duration per species was negatively correlated with, species richness. The inter-correlation among trait variables in phylogenetic independent contrasts was calculated and examined. Both foraging height and relative eye size were selected as positively explanatory factors, but no dietary effects were detected, for chorus onsets. Dawn singing onsets also tended to delay as decreasing log (eye sizes) that, however, was not selected with enough explanatory power. The positive relationship of chorus onsets versus relative eye sizes contradicts our prediction, yet the negative correlation of relative eye sizes with log (eye sizes) indicates an allometric constraint on eye sizes along with increasing body sizes. Lower-layer species initiated singing earlier than upper-layer species, which complies with the positive correlation of onsets with foraging heights and supports our prediction. This pattern may be condition-specific and more likely occurs in forests lacking a sufficient canopy height and layering and a distinct light difference among forest layers. Foraging heights were additionally found negatively correlated with canopy coverage and slightly positively correlated with ground coverage of perches. Our results concord that foraging height is a relevant factor as eye size in determining the onset and sequence of dawn chorus, yet, suggest that forest settings and vegetation structure may likely complicate the prediction.

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Introduction

Many bird species, notably but not exclusively the songbirds (Passeriformes), use vocal sounds to fulfill intersexual interactions, such as self-advertising and stimulating mates (*e.g.*, Kroodsmma, 1976; Otter and Ratcliffe, 1993; Welling *et al.*, 1995), or intrasexual interactions like social communication and acquiring or defending territory (Amrhein and Erne, 2006; Foote *et al.*, 2008), or both. This behaviour is particularly prominent at dawn and for males in the breeding seasons (Slagsvold, 1996; Kunc *et al.*, 2005; McNeil *et al.*, 2005; Amrhein and Erne, 2006), and often turns into a collective phenomenon known as dawn chorus.

While the association of dawn chorus with the breeding seasons offers ontogenetic (*i.e.*, sexual maturity) and mechanistic (*i.e.*, hormone) explanations, the reasons why male birds engage in vocal activity vigorously at dawn appear to be due to, at least in part, certain proximate physical factors that are not mutually exclusive, and also carry functional perspectives. Lower temperatures and high humidity at dawn may restrict

activity of both birds and their prey (Avery and Krebs, 1984), but also that of predators that otherwise would be attracted to bird calls. In contrast, lower wind speed and background noise levels in this period are more energetic-efficient and favourable for sound travel with consistency (*i.e.*, the acoustic transmission hypothesis; Henwood and Fabrick, 1979; Cuthill and Macdonald, 1990; Brown and Handford, 2003; but see Dabelsteen and Mathevon, 2002). The limited light level at dawn prohibits diurnal birds from many daytime activities, such as foraging (*i.e.*, the inefficient foraging hypothesis; Kacelnik, 1979; Kacelnik and Krebs, 1982) or social contacts with one another (Cuthill and Macdonald, 1990), but the latter can be achieved vocally (Kacelnik, 1979; Amrhein and Erne, 2006; Foote *et al.*, 2008).

Temporal variation in dawn chorus may also be caused by proximate factors such as light availability that is usually, but not completely (see Kempenaers *et al.*, 2010; Da Silva *et al.*, 2015), related to time, weather, and vegetation (Berg *et al.*, 2006). Overnight birds may have surplus energy from previous feeding to sustain the night time fast and a lower temperature, which helps to explain why birds can afford to delay foraging and instead engage in singing at dawn (*i.e.*, energy storage stochasticity hypothesis; Hutchinson, 2002). This reasoning concerns more on the variability of participation, so individual variation in quality or status can be assessed (*i.e.*, state-dependent), but does not directly address the sequence and variation at dawn singing among species (Cuthill and Macdonald, 1990; Berg *et al.*, 2006). Masking of signals, such as by noise, carry additional cost and negatively impact avian reproductive success (Halfwerk *et al.*, 2011). Simultaneous songs by various species may also interfere with each other and affect the transmission effectiveness, thus a temporal asynchrony to avoid signal overlapping should be favored (Cody and Brown, 1969; Ficken *et al.*, 1974; Popp *et al.*, 1985).

Species may differ in their sensitivity to light, therefore sense the light level effectively at slightly different time or place (Thomas *et al.*, 2002; McNeil *et al.*, 2005; Berg *et al.*, 2006). This has been noted particularly for species in forested areas (*e.g.*, Popp *et al.*, 1985). In addition, singing attracts predators as well as potential mates, but a bird may lower its alert to potential hazards while singing. Thus, birds should be selected for to sing only if they are able to scan sufficiently the surrounding at a certain light level (Thomas *et al.*, 2002). It is expected that the earlier a bird sings at dawn, the better it is able to detect the surroundings

even at dim light (Hutchinson, 2002; Thomas *et al.*, 2002; McNeil *et al.*, 2005), which may be determined by a bird's visual anatomical features, but also associated with the surrounding settings and light levels where a bird is situated.

Birds with larger eyes tend to have earlier dawn singing (Thomas *et al.*, 2002; McNeil *et al.*, 2005). This is supported by anatomical relationships that larger-eyed birds own higher numbers of light-sensitive visual cells on the retina, a thicker inner retinal layer, and more neuron synapses, all these indicating a better visual sensitivity and higher resolution for low light conditions (Hart, 2001a, 2001b; Garamszegi *et al.*, 2002; McNeil *et al.*, 2005). Forest layers, due to the amount of foliage overhead, can have different light levels, and birds perching at a higher place usually receive a richer light availability. Yet, the position chosen by a bird for signaling (*i.e.*, songposts) may not be the same as, and often is higher than, that used for roosting and foraging (Hunter, 1980; Barker and Menzies, 2009). Most forest birds foraging at lower-layers or on the ground also tend to roost at higher places or even up to the canopy at night. In contrast, species adapted to constantly foraging at lower heights or on the ground may have evolved a higher visual sensitivity and acuity that allows them to sense better in dim light earlier (McNeil *et al.*, 2005; Thomas *et al.*, 2006).

Further, avian foraging relies heavily on visual cues, so different visual sensitivities may have evolved in species adapted to different diets (Hart, 2001b; Garamszegi *et al.*, 2002; Fernández-Juricic *et al.*, 2004). Compared to plant resources, prey are often vigilant, requiring rapid detection by birds, or cryptic in coloration or pattern, both require substantial light levels to detect. In case of insect swarms, aerial insectivores are generally equipped with a larger degree of movement sensitivity and resolution-related double cone cells for detecting prey in movement at fast speeds (Hart, 2001a). Thus, predatory birds should have better visual capacity and light sensitivity to effectively search for prey, particularly for foraging within a forest setting (Thomas *et al.*, 2002; McNeil *et al.*, 2005).

We examined the pattern and seasonal variation of avian dawn chorus in a tropical montane forest in Taiwan, where related information is extremely sparse. We tested whether species richness and the assemblage composition affect dawn chorus, and predicted that a greater number of species engaging in dawn chorus prolong the overall chorus duration but shorten individual species singing lengths. We also tested the hypothesis that the sequence of a dawn chorus can be

determined by eye size, foraging height, and diet of birds, and predicted that earlier dawn singing is associated with species of larger relative eye size. In addition, we predicted that birds primarily foraging at forest floor or lower heights will sing earlier, and predatory birds will have an earlier dawn singing than plant-eating species.

Materials and methods

Study sites

Field work took place between March and October, 2007 and 2008, in the Liouguei Experimental Forest (LEF) surrounding the Shanping Field Station (23°55'N, 120°41'E, ca. 993 ha in area and 550–1200 m in elevations; Taiwan Forestry Research Institute, TFRI) in Kaohsiung, southern Taiwan. The area is characterized by monthly mean temperature of around 16 °C in January and 24 °C in July–August. Rainfall occurs mainly in the monsoon season and often is accompanied by typhoons from May to September, with an accumulated amount of nearly 3000 mm that accounts for over 85% of the total annual precipitation (about 3500 mm; Shanping Weather Station data, TFRI).

Secondary forests constitute the vegetation of the study sites, composed of 134 families, 71 species of pteridophytes, 23 species of gymnosperms, 128 species of monocotyledons, and 463 species of dicotyledons (Wang 1991). Dominant vegetation on high hills included mainly Lauraceae [*e.g.*, *Beilschmiedia erythrophloia* (Hayata), *Machilus japonica* Siebold & Zucc., and *Cinnamomum camphora* (L.) J. Presl.] and Fagaceae [*e.g.*, *Castanopsis carlesii* (Hemsl.) Hayata, *C. indica* (Roxb. ex Lindl.) A. DC., and *Cyclobalanopsis glauca* Thunb.], whereas Moraceae (*e.g.*, *Ficus superba* Miq., *F. septica* Burm.f., *F. benjamina* L.1767) took over along with *Broussonetia papyrifera* (L.) Vent., *Mallotus paniculatus* (Lam.) Mull.Arg., and *Trema orientalis* (L.) Blume. in riparian valleys.

Dawn chorus sampling

We monitored dawn chorus at eight replicate sites that were in similar vegetation structure. Any two proximate sites were beyond 250 m apart in distance, and all sites were away from the main pass or any trails, and thus from potential human disturbance or noise. In each month we conducted two bi-weekly sessions of

4-day dawn sampling, one site each day. The sampling in each session occurred in consecutive four days as possible, and in clear stable weather conditions or nearly so. We randomly alternated the order of site among census days within each month. At each site, we chose a relatively open forest gap that was at least 20 m in radius to allow for auditory monitoring, and visual observations when light level permitted.

Sampling started 1.5 hr before sunrise at local times (the Central Weather Bureau data, Taiwan), and lasted until dawn singing ended, defined as 20 min after the last singing bout of the last species heard, usually near 08:00. We recorded the onset and end times of each bout of dawn chorus sequences to seconds using a stop watch (Thompson *et al.*, 1994), and the species that made songs, following Severinghaus *et al.* (2012) and BirdLife International (2014) for the nomenclature. We also tallied song numbers in each bout by a counter. Two consecutive bouts from the same species were distinguished by a silent period, mostly over 10 seconds, or occasionally (less than 3.7%, $n = 5510$) when two bouts with a pause timed shorter than 10 seconds but were from two identifiable source directions. We acknowledged that our measurements might have been underestimations, but only in a few occasions (3%, $n = 5510$) where singing by two birds of the same species overlapped in time. Prior to our auditory sampling observers were trained and tested for accuracy and consistency by data collected using a super-cardioid condenser microphone (ME66/K6, Sennheiser Electronic, Wedemark, Germany) and a field recorder (Fostex FR-2, Foster Electric Corporation, Tokyo, Japan). The microphone was positioned on a tripod 1.5 m above the ground and pointed to the most proximate direction of bird sounds, where the sound with maximum intensity was heard. We recorded light level at the onset of each bout of singing using a light meter (1339 Pro, TES Electronic Corporation, Taipei, Taiwan), and humidity and temperature in the beginning and the end of each census by a combined Humidity and Temperature Indicator (WISEWIND, Centenary Materials, Hsinchu, Taiwan).

Eye size and morphometric measurements

We estimated the eye size of bird species that were recorded in our sites by measuring skull specimens of museum collections (Chen, 2010). We measured orbital morphometric parameters, including the maximum length along the long and short axes of the orbit socket, and the length and width of skull. Eye size in

volume (ES , mm^3) was estimated using $ES = 2 \times 1.33\pi a^2 b$ (Garamszegi *et al.*, 2002), where a and b each represents the long the short axial length of an eye socket. This estimate was strongly correlated ($r = 0.97$, $p < 0.05$; Chen, 2010) to that obtained from the approach of applying a series of spherical plastic balls of different sizes to best fit with the eye socket of the birds (Brooke *et al.*, 1999; Thomas *et al.*, 2006). For few species where proper skull specimens were inadequate or completely lacking, we adopted live bird measurements as a substitute. Birds were mist-netted along trails surrounding our study area, and we measured the maximum lengths along the long and short axes of eye socket (to 0.1 mm) using an electronic caliper (SV-03 Digital Vernier Caliper, E-BASE, Yunlin, Taiwan). Our netting complied with the legal requirements of Taiwan and the guidelines for the use of animals in research (Sherwin, 2006) throughout our procedures. The orbital measurements (mm) from skull specimens were correlated to direct eye measurements of live birds in both the long axis ($r = 0.52$, $p < 0.05$) and the short axis ($r = 0.80$, $p < 0.05$; Chen, 2010), respectively. We corrected our eye measurements using these correlations, but kept the use of this measure to a necessary minimum for a better consistency. We used log-transformed eye size (LES) and its relative value (RES), $\log(\text{eye size})/\log(\text{body mass})$, for further analyses. The latter considered the allometric effect and was corrected for body size (Berg *et al.*, 2006).

Foraging perch heights and food habits

For each species engaged in dawn chorus, we located and sighted individuals to record the aspect and the perching locations between 08:00 and 10:00 on the same morning. The distances and heights of perches were visually estimated using on site reference marks, and later corrected by a laser distance meter (Leica DISTO A5). The perch heights were further categorized to up- (≥ 7 m), mid- (≥ 1.5 m to < 7 m), and bottom (< 1.5 m) layers. We additionally recorded the species and estimated the height of the perch trees, and measured habitat variables surrounding a perch, including canopy and ground coverage.

We determined birds' diets first by onsite observations after dawn chorus during the study period (Chen, 2010), but not every species' foraging was adequately documented due to practical difficulties. We further incorporated data retrieved from Ding *et al.* (2008), Wu (2008), and those compiled in Severinghaus *et al.* (2012). We used data that were collected by a similar

method in mid-elevation montane areas, prioritizing those with seasons and locations proximate to this study, or adopting their averages when no distinction could be made. We used the item proportions of animal contents at 25% and 75% as dividing levels to further classify diets into three classes: animal-eating ($\geq 75\%$), omnivores (≥ 25 but $< 75\%$), and plant-eating ($< 25\%$; Remsen and Parker, 1984). Animal contents here refer only to insects and non-insect invertebrates. We excluded true carnivores, and birds that are active nocturnally or often vocalize in the night, such as night herons, were also excluded.

Phylogenetic independent contrasts

We grouped species engaging in the dawn chorus into three rooted and unambiguous clades: Galliformes (Phasianidae), Piciformes (Picidae and Ramphastidae), and passerines. To assure independence of observations, we calculated Felsenstein's (1985) phylogenetic independent contrasts in character traits. The contrast calculation was conducted using a phylogenetic hypothesis based on Sibley and Ahlquist (1990), and incorporating recent treatments on the Old World babblers (Timaliidae; Baker *et al.*, 2001; Cibois, 2003; Collar and Robson, 2007), and the results from cytochrome oxidase subunit I (COI) sequence analyses (CT Yao and SH Li, unpubl. data) for interspecific relationships within this group. Phylogenetic independent contrasts were calculated using COMPARE, assuming that the character evolution can be described in a random walk mode, equal branch lengths, and negligible within species variation compared to that among species (Martins, 2004).

Data analyses

Data are presented as mean \pm standard error (SE) unless otherwise noted. We performed statistical analyses using MINITAB 14.12 (Minitab 2003) and SPSS 12.0.1 (SPSS 2000) for Windows 2000, and set the significance level at $\alpha = 0.05$. We corrected onset times relative to the local sunrise to obtain the relative onset times of dawn singing, and calculated duration of dawn signing, for each species and each dawn chorus sequence (Lein, 2007; Liu and Kroodsmas, 2007; Foote *et al.*, 2008). We adopted multivariate analysis of variance (MANOVA) with Wilks' Λ to examine the temporal (sampling month and year) and spatial (elevation) variation in onset time, total chorus duration, and mean chorus duration. Analysis of variance (ANOVA)

was used to examine the differences in onset time among birds of different eye-size groups and foraging heights. In both analyses, we conducted post-hoc comparisons using Fisher's least significant difference (LSD) to locate differences. Pearson's correlation analysis was used to examine the relationships of onset time and chorus duration with number of species engaged in dawn singing. The inter-correlation among trait variables, eye size, perching height, and diet content, in independent contrasts was examined using COMPARE (Martins, 2004), and tested by Student's $t = r/\sqrt{(1 - r^2)/\sqrt{(n - 2)}}$, where r is correlation coefficient and n is sample size. We restricted this analysis to species that associated ecological and morphological data were fully available and that occurred in all sampling sites. We further adopted the contrasts to examine the effects of eye size, perching height, and food habit on onset of dawn signing among species using stepwise regression analysis, if each of the correlation coefficients between paired variables was less than

0.8, setting $\alpha = 0.05$ for adding a variable to the model (Zar, 2010).

Results

We recorded 112 dawn chorus sequences comprising of 5510 bouts of songs or calls (mean: 49.2 ± 1.94 , range: 4–90), made by 21 species of 15 passerine families, two species of Piciformes, and two species of Galliformes (Table 1). Rusty-cheeked (*Pomatorhinus erythrogenys* Vigors 1832) and Streak-breasted Scimitar Babblers (*P. ruficollis* Hodgson 1836), Grey-cheeked Fulvettas (*Alcippe morrisonia* Swinhoe 1863), Taiwan Barbets [*Psilopogon nuchalis* (Gould, 1863)], and Taiwan Whistling Thrushes (*Myophonus insularis* Gould, 1862) were the most frequent species engaging in dawn chorus. They were followed by Taiwan Partridges [*Arborophila crudigularis* (Swinhoe, 1864)], White-bellied Yuhinas [*Erpornis zantholeuca*

Table 1. Relative occurrence (%), mean (\pm SE) perching height (m), relative eye size (see the text), and diet (percent animal content) of the 25 species of birds studied. Sample sizes of each species for height and eye size are in parentheses after each value.

†B: bottom-layer, M: mid-layer, U: upper-layer; ‡S: small (size ≤ 2.4), M: medium ($2.4 < \text{size} \leq 3.4$), and L: large (size > 3.4); §A: animal-eater, O: omnivores, P: plant-eater.

Species	Rel. Occur.	Height†	Rel. Eye Size‡	Diet§	
Campephagidae	<i>Pericrocotus solaris</i>	4.61	15.85 ± 1.36^U (38)	3.26 ± 0.05^L (5)	87.5 ^A
Corvidae	<i>Dendrocitta formosae</i>	3.94	9.42 ± 0.76^U (44)	2.32 ± 0.03^S (5)	61.3 ^O
	<i>Urocissa caerulea</i>	1.93	8.22 ± 1.37^U (9)	2.21^S (1)	61.0 ^O
	<i>Dicrurus aeneus</i>	3.35	13.55 ± 1.86^U (9)	2.93^M (1)	100.0 ^A
Leiothrichidae	<i>Yuhina brunneiceps</i>	1.51	10.00^U (1)	3.52 ± 0.02^L (29)	30.6 ^O
Megalaimidae	<i>Psilopogon nuchalis</i>	7.54	11.19 ± 0.73^U (71)	2.35 ± 0.03^S (13)	10.0 ^P
Monarchidae	<i>Hypothymis azurea</i>	3.69	4.13 ± 0.35^M (29)	3.56 ± 0.11^L (3)	95.7 ^A
Motacillidae	<i>Motacilla alba</i>	< 0.1	---	2.81 ± 0.09^M (3)	100.0 ^A
Muscicapidae	<i>Myiomela leucura</i>	0.92	0.46 ± 0.26^B (3)	2.94 ± 0.02^M (20)	100.0 ^A
	<i>Niltava vivida</i>	0.84	13.00^U (1)	3.15 ± 0.14^M (4)	100.0 ^A
	<i>Rhyacornis fuliginosa</i>	1.42	0.00 ± 0.00^B (8)	3.42 ± 0.08^L (5)	100.0 ^A
	<i>Parus monticolus</i>	0.25	---	3.65 ± 0.13^L (14)	100.0 ^A
Pellorneidae	<i>Alcippe brunnea</i>	4.86	0.37 ± 0.10^B (9)	3.26 ± 0.07^L (5)	100.0 ^A
	<i>Alcippe morrisonia</i>	7.54	3.95 ± 0.20^M (99)	3.45 ± 0.02^L (58)	59.2 ^O
Phasianidae	<i>Arborophila crudigularis</i>	6.2	0.25 ± 0.25^B (2)	---	> 50.0 ^O
	<i>Bambusicola thoracicus</i>	4.52	0.04 ± 0.04^B (11)	1.79 ± 0.03^S (3)	93.0 ^A
Picidae	<i>Dendrocopos canicapillus</i>	2.93	9.33 ± 1.53^U (18)	3.05^M (1)	100.0 ^A
Pycnonotidae	<i>Hypsipetes leucocephalus</i>	5.28	16.73 ± 1.37^U (42)	2.47 ± 0.03^M (5)	20.4 ^P
Sylviidae	<i>Abroscopus albogularis</i>	2.01	4.20 ± 1.20^M (5)	5.05 ± 0.09^L (13)	100.0 ^A
Timaliidae	<i>Heterophasia auricularis</i>	1.59	7.38 ± 1.18^U (9)	2.48 ± 0.03^M (22)	55.9 ^O
	<i>Pomatorhinus erythrogenys</i>	7.79	0.67 ± 0.09^B (16)	2.32 ± 0.13^S (3)	100.0 ^A
	<i>Pomatorhinus ruficollis</i>	7.71	1.42 ± 0.20^B (52)	2.67 ± 0.04^M (11)	60.6 ^O
	<i>Stachyridopsis ruficeps</i>	5.95	1.14 ± 0.20^B (11)	3.58 ± 0.05^L (24)	72.9 ^O
Turdidae	<i>Myiophoneus insularis</i>	7.54	0.77 ± 0.22^B (23)	2.26 ± 0.08^S (4)	100.0 ^A
Vireonidae	<i>Erpornis zantholeuca</i>	6.03	5.07 ± 0.30^M (49)	3.80 ± 0.09^L (7)	95.5 ^A

(Blyth, 1844)], Rufous-capped Babblers (*Stachyridopsis ruficeps* Blyth, 1847), and Black Bulbuls (*Hypsipetes leucocephalus* Müller, 1776). Each of these species accounted for greater than 5% and collectively nearly 62% of the total occurrence in dawn chorus (Table 1).

Dawn singing pattern and temporal variation

A dawn chorus sequence began from 74.0 to 11.6 min before sunrise (mean 30.86 ± 0.81 min), and lasted from 33.65 to 233.03 min (115.29 ± 4.10 min; $n = 112$). Both the relative onset times and the chorus duration were affected by the sampling year (MANOVA: Wilks' $\Lambda = 0.833$, $F_{(3,68)} = 4.532$, $p = 0.006$) and month (Wilks' $\Lambda = 0.542$, $F_{(15,188)} = 3.113$, $p < 0.001$) with in-

teraction (Wilks' $\Lambda = 0.537$, $F_{(15,188)} = 3.165$, $p < 0.001$), but not by the elevation range of sites (Wilks' $\Lambda = 0.918$, $F_{(3,68)} = 2.037$, $p = 0.117$). Relative onset times advanced the most in May (Fisher's LSD, May > April, $p < 0.05$) and then progressively delayed toward August (all p values < 0.005 or 0.001). In contrast, mean dawn chorus last longer in early summer and peaked in June (Fisher's LSD, June > March, $p < 0.05$; June > July, $p < 0.05$; Fig. 1). The dawn chorus duration was positively ($r = 0.34$, $F_{(1,92)} = 8.697$, $p < 0.005$; Fig. 2a), but the mean singing duration per species negatively ($r = 0.28$, $F_{(1,92)} = 7.513$, $p < 0.01$; Fig. 2b), correlated to the number of bird species engaging in a chorus, whereas relative onset times showed no correlation ($r = 0.118$, $F_{(1,92)} = 0.02$, $p = 0.887$).

Among species, *M. insularis* initiated the earliest singing and had the longest duration. It was followed by *A. morrisonia* and *P. erythrognys*, and then by *A. crudigularis* and *P. ruficollis* in onset time, with their mean onsets earlier than or close to the sunrise, while all other species started singing 5 min or longer after the sunrise. In contrast, singing duration of *A. crudigularis* and *P. ruficollis* was among the shortest (Fig. 3). When only the singing of each species engaging as the first starter in a chorus was considered, the duration and relative onsets of dawn singing also fluctuated among species (MANOVA: Wilks' $\Lambda = 0.73$, $F_{(8,192)} = 4.067$, $p < 0.001$). First song of *A. morrisonia* (44.16 ± 15.16 min before sunrise) exceeded *M. insularis* (30.51 ± 0.65 min before sunrise; Fisher's LSD, $p < 0.05$) in onset time, and was earlier than *A. crudigularis* (27.07 ± 0.55 min before sunrise; Fisher's LSD, $p < 0.05$), but not significantly different from *P. erythrognys* (35.03 ± 17.91 min before sunrise) and *P. ruficollis* (30.29 ± 8.07 min before sunrise). The singing duration of *A.*

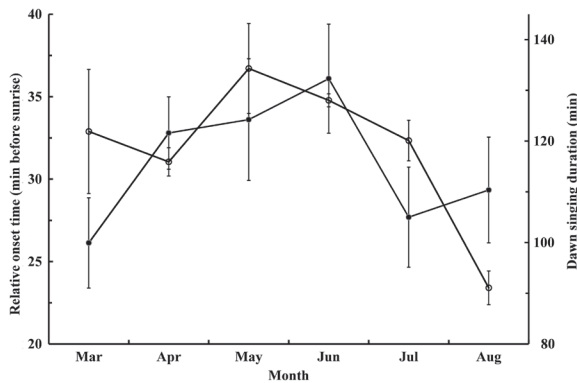


Fig. 1. Mean (\pm SE) relative onset times (min; \circ) of first song and chorus duration (min; \bullet) at dawn by birds in the LEF sites over months (onset times: Aug < Mar, Apr, May, June, and Jul, all p values < 0.005; singing lengths: Jun > Mar, Jun > Jul, p values < 0.05).

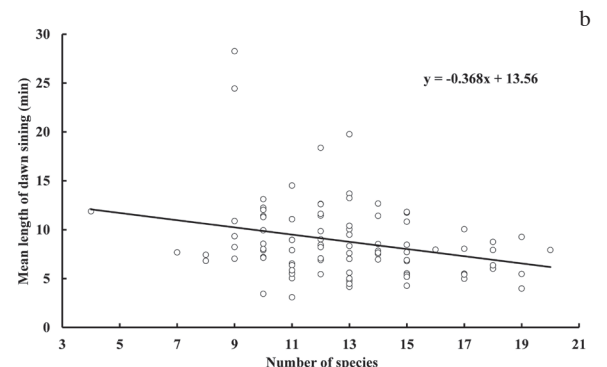
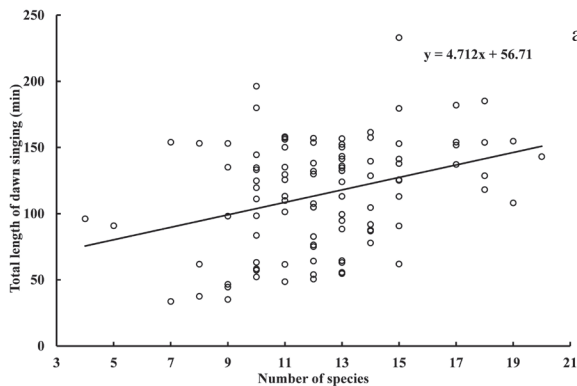


Fig. 2. The correlation of (a) total chorus length and (b) mean singing length per species to number of species engaged in dawn chorus in the Liouguei Experimental Forest.

morrisonia (47.51 ± 11.08 min; Fisher's LSD, $p < 0.001$) and *P. ruficollis* (31.8 ± 8.92 min) also outlast that of *M. insularis* (17.56 ± 1.11 min; Fisher's LSD, $p < 0.05$) and *A. crudigularis* (2.81 ± 2.6 min; Fisher's LSD, $p < 0.005$).

Independent contrasts

Phylogenetic independent contrasts in onset time of dawn singing were not correlated to contrasts of height

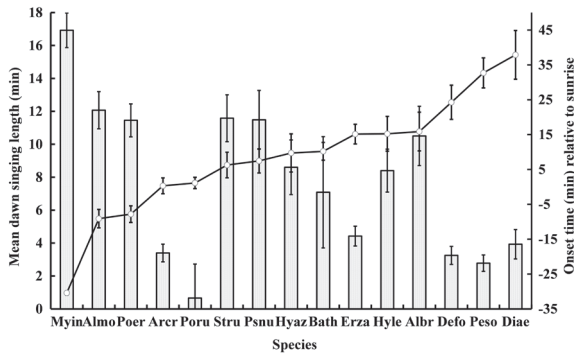


Fig. 3. Mean (\pm SE) dawn singing duration (min; \square) and relative onset time (min; $-\circ-$) of 15 species of birds that occurred in both years and with the highest occurrence frequency. Species name abbreviation (sample size) are: Albr, *Alcippe brunnea* (60); Almo, *Alcippe morrisonia* (106); Arcr, *Arborophila crudigularis* (86); Bath, *Bambusicola thoracicus* (60); Defo, *Dendrocitta formosae* (62); Diae, *Dicrurus aeneus* (44); Erza, *Erpornis zantholeuca* (82); Hyle, *Hypsipetes leucocephalus* (66); Hyaz, *Hypothymis azurea* (48); Psnu, *Psilopogon nuchalis* (101); Myin, *Myiophonus insularis* (105); Peso, *Pericrocotus solaris* (64); Poer, *Pomatorhinus erythrognys* (109); Poru, *Pomatorhinus ruficollis* (106); Stru, *Stachyridopsis ruficeps* (78).

($r = 0.43, t = 2.02, p = 0.06$), diet ($r = 0.15, t = 0.64, p = 0.53$), or log (eye size) ($r = -0.01, t = -0.04, p = 0.97$), and barely with relative eye size ($r = 0.45, t = 2.14, p = 0.05$; all $d.f. = 18$). While foraging height contrasts were slightly negatively correlated with diet contrasts ($r = -0.51, t = -2.52, p < 0.05$), the contrasts of log (eye size) (LES) and relative eye size (RES) was neither correlated with that of foraging heights (LES: $r = 0.06, t = 0.26, p = 0.80$; RES: $r = -0.10, t = -0.43, p = 0.68$) nor with diet contrasts (LES: $r = 0.20, t = 0.87, p = 0.40$; RES: $r = 0.44, t = 2.08, p = 0.06$). Thus, foraging height and percent animal content in diet were adopted with the log (eye size) (model I) and the relative eye size (model II), respectively, in further stepwise multiple regression analysis.

The effects of eye size, foraging height, and diet

In model I, foraging height was firstly chosen ($R^2 = 0.28, F_{(1,17)} = 6.53, \beta = 0.53, t = 2.56, p < 0.05$), the log (eye size) barely selected ($\beta = -0.38, t = -1.96, p = 0.07$), and the percent animal content in diet not chosen ($\beta = 0.33, t = 1.48, p = 0.16$). Model II, however, picked both foraging height ($\beta = 0.53, t = 3.21, p = 0.005$) and relative eye size ($\beta = 0.5, t = 2.93, p = 0.01; R^2 = 0.53, F_{(2,16)} = 9.01, p < 0.01$), with the former first chosen and 28% of variation in dawn singing explained, and adding relative eye size increased the power of explanation by 0.25.

Among species, mean dawn singing onset time delayed with increasing relative eye size ($r = 0.48, p < 0.05$; Fig. 4a), which resulted from a negative correlation between log (eye size) and relative eye size ($r = -0.81, p < 0.05$). Onset time also delayed as increasing foraging height ($r = 0.54, p < 0.05$; Fig. 4b), and this

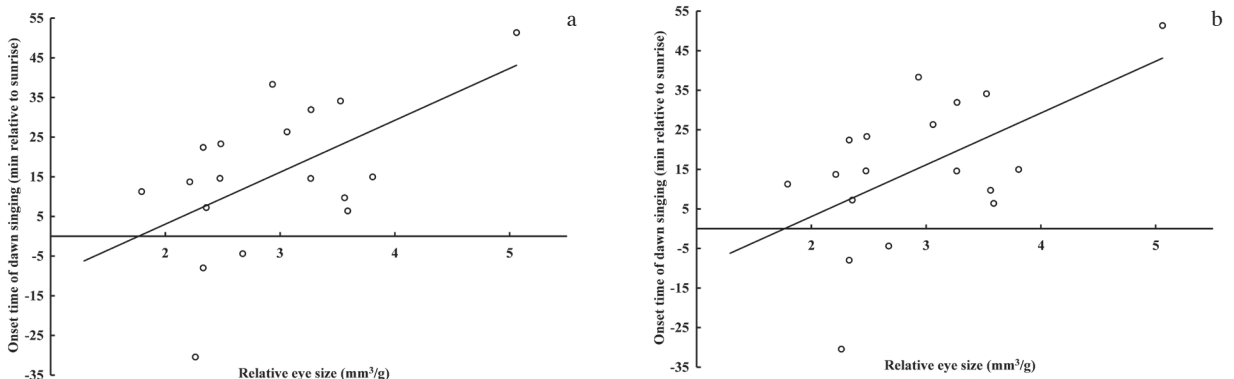


Fig. 4. The correlation between dawn singing onsets of birds and (a) relative eye sizes and (b) foraging heights in the Liouguei Experimental Forest.

held when data were restricted to passerines ($r = 0.57$, $p < 0.05$). Birds customarily associated with different forest layers initiated singing at different times (ANOVA: $F_{(2,16)} = 4.51$, $p < 0.05$), with bottom-layer species starting earlier (-1.74 ± 6.76 min, $n = 6$) than those of up-layer (23.56 ± 3.43 min, $n = 9$; Fisher's LSD, $p < 0.05$), but neither group differed from birds in the mid-layer (16.72 ± 12.65 min, $n = 4$). Eye size also varied among birds associated with different forest layers (MANOVA: Wilks' $\Lambda = 0.49$, $F_{(4,30)} = 3.219$, $p < 0.05$) but in different ways; while log (eye size) was smaller in mid-layer (3.72 ± 0.05 ; Fisher's LSD, $p < 0.05$) than in up- (4.15 ± 0.12) and bottom-layer birds (4.11 ± 0.14), relative eye size was larger in mid-layer (3.96 ± 0.36) than up- (2.73 ± 0.16) and bottom-layer birds (2.68 ± 0.24 ; Fisher's LSD, $p < 0.005$). Foraging height, however, was found relating to vegetation variables ($R^2 = 0.75$, $F_{(4,15)} = 11.01$, $p < 0.001$), specifically negatively with canopy cover ($t = -6.48$, $p < 0.001$) and positively with ground cover ($t = 2.92$, $p < 0.05$), but not strongly with the canopy depth ($t = -0.48$, $p = 0.64$) or a tree's distance to the forest edge ($t = -0.11$, $p = 0.91$).

Discussion

Onset and duration of avian dawn chorus in the LEF forest peaked in the prime breeding season of most common birds in this region (Severinghaus *et al.*, 2012). This is consistent with the conclusion that song activity at dawn is mainly associated with female fertility cycles (Mace, 1987). Those birds that sang earlier were mostly insectivores (e.g., *M. insularis*, *P. erythrogeus*, and *A. crudigularis*) or omnivores (e.g., *P. ruficollis* and *S. ruficeps*) active on the forest floor. Upper-layer and plant eating *H. leucocephalus* and *M. nuchalis* appeared in the middle, while most other up-layer dwellers like Grey Tree-pies (*Dendrocitta formosae* Swinhoe, 1863), Bronzed Drongoes (*Dicrurus aeneus* Vieillot, 1817), and Grey-chinned Minivets (*Pericrocotus solaris* Blyth 1846) started relatively late, in a chorus. Mid-layer species that retain a greater chance to explore both upward and downward are presumably equipped with a greater visual or behavioral flexibility, not surprisingly showed a greater variation in their onsets within a chorus sequence. This included the secondly ranked *A. morrisonia* and species in the middle of a chorus, like Black-naped Monarchs [*Hypothymis azurea* (Boddaert, 1783)] and *E. zantholeuca*, while other mid-layer dwellers started late in dawn chorus. Interestingly, *A. morrisonia*, *P. erythrogeus*

and *P. ruficollis* significantly advanced their onsets when engaging as the first birds singing in a dawn chorus, but their overall mean onset times usually were a little later than those of typical first starters. This, together with the confirmed prediction that increasing numbers of species engaged in dawn singing prolonged the chorus duration but decreased the singing duration of each species, suggest that subtle species interactions, such as interspecific hierarchy or competing for singing posts, may be involved in dawn chorus and warrant further detailed investigations.

Our observations and regression results indicate that foraging heights and relative eye sizes, but not log (eye size) and diets, are the more relevant factors affecting the onsets and sequence of avian dawn chorus. This is largely consistent with the notion of a similar influence of ecological factors compared to morphological factors on dawn singing, and supports the speculation that the eye morphology may be more conservative in evolution (Berg *et al.*, 2006). Although with a relatively smaller data set, our results also reveal that species active at lower heights start to sing earlier at dawn, and supports our prediction. This, however, contradicts to that of Berg *et al.* (2006) showing the opposite and the discrepancy demands explanations.

Heights of birds that make the first songs at dawn are often difficult, if not completely impossible, to observe and measure because of light limitation. Thus foraging heights were adopted as a proxy to infer the environment conditions where birds' singing may be associated with (Berg *et al.*, 2006; this study), but for different reasoning. Birds perching at higher places may receive a greater amount of light and earlier. Yet, birds primarily foraging at certain heights may not roost overnight at the same level. Most birds, including ground foragers like sparrows, pigeons, and herons, roost at higher places at night presumably for the sake of reducing predation risk from the ground. Low-layer or ground foragers could also move upper at dawn to perch and then sing at a light-exposed and more energetic-efficient location. For instance, we observed understory foragers *P. erythrogeus* singing on the top of standing dead tree trunks at places with sparser vegetation, and *M. insularis* singing up to 4 m height, both higher than their typical foraging heights (Chen, 2010). The genus name of Taiwan Partirdges (*Arborophila*), although a typical forest floor forager (Severinghaus *et al.*, 2012), also implies a high-perch association. We reasoned and interpreted foraging heights as the height level where primarily associated species with suffi-

cient light sensitivity capable of sensing available dim light at dawn before foraging, instead of the height level with its actual light availability at sighting. This concurs with the inefficient foraging hypothesis (Kacelnik and Krebs, 1982).

Under this reasoning, low-layer or ground foragers with sharper sensitivity could sense dim light and initiate singing earlier than upper layer species when roosting at a higher, similar, or even slightly lower level. Only when birds associated with different forest heights partition the layers drastically that upper-layer foragers roost at much higher perches, the light difference between the up and lower levels may outweigh that in light sensitivity between species of different heights. Tree canopies of Neotropical rain forests in previous dawn chorus studies often reach 25 m or more, easily creating dramatic light gradients between the canopy layer and the forest floor as much as two-fold of difference (e.g., Brown and Handford, 2003; Berg *et al.*, 2006). This likely would increase the chance of upper-layer foragers with higher night perches singing at dawn earlier.

In contrast, our study sites comprised of secondary forests where canopy reached 10–12 m only, with less distinctive inter-layer vegetation structure. The difference in light level between the understory and canopy layers was less dramatic, and may reduce the time difference in receiving sufficient light levels to trigger dawn singing. A few meters of shift in this forest setting by species foraging at lower levels would make the actual temporal difference in light availability insignificant, but the species difference in light sensitivity may still do. This thus far is supported by our observations in Fengongshan, an area about 1800 m in elevation and 5 km from our sites, where comprised of primary forests of tree heights above 20 m. Top canopy dwellers like Steere's Liocichla *Liocichla steerii* Swinhoe 1877 and White-eared Sibia *Heterophasia auricularis* (Swinhoe, 1864) appeared to sing earlier. Those associated with mid-to-upper layer followed, such as Rufous-faced Warbler *Abroscopus albogularis*, *P. nuchalis*, and Taiwan Yuhina *Yuhina brunneiceps*, and were further followed by mid and bottom layer species, including *A. morrisonia*, *P. erythroge-nys*, *P. ruficollis*, *A. crudigularis*, and *S. ruficeps*, with less differences (YF Lee, unpubl. data).

A greater eye size should contain more visual cells, and potentially is more capable of detecting light in a dim environment (McNeil *et al.*, 2005). Yet, our data showed a positive correlation of relative eye sizes to dawn singing onsets, which contradicts our prediction.

Species in our study comprised of a larger number of single-species families, except timaliids and muscicapids comprising of multiple species. Those of Thomas *et al.* (2002) were mainly of sylviids and muscicapids, whereas species in Berg *et al.* (2006) were mostly distinctive to the neo-tropics. Variability among different species lineages might have complicated this discrepancy and requires further investigations. Nonetheless, relative eye sizes were tightly negatively correlated to log eye sizes, resulting in a smaller relative eye size as eye size growing along with body size, an indication of allometric growth of eyes versus body sizes in birds. This is consistent with the finding across 104 bird family (Brooke *et al.*, 1999). In contrast, although the log eye size was only barely selected by the model, but appeared negatively correlated to the dawn singing onset, which still concurs with our prediction.

The light sensitivity of birds may also be affected by anatomical features of eyes other than size. Bergamin *et al.* (1998) confirmed that in humans brown iris is associated with greater pupillary contraction amplitude, time, contraction velocity, and re-dilation than paler, such as blue, iris. The relationship of iris with light and visual sensitivity in birds is not yet well established. Avian species that are typically adapted to nocturnal activity, and thus are presumably with higher light sensitivity (*i.e.*, Strigidae), have either reddish brown iris, such as Collared Scops Owls (*Otus bakamoena* Pennant, 1769), or pale yellowish iris, such as Mountain Scops Owls [*O. spilocephalus* (Blyth 1846)] and Collared Owlets [*Glaucidium brodiei* (Burton, 1836)]. Those earliest species engaging in dawn chorus in our study also have either reddish (e.g., *M. insularis* and *A. morrisonia*) or pale yellowish iris (e.g., *P. erythroge-nys* and *P. ruficollis*). In addition, the tapetum lucidum, a reflective layer in retina, may increase the amount of light received by photosensitive cells and allow a better vision in low light conditions, and requires further detailed studies.

In comparison, diets of birds did not play any significant effects as predicted. Most of the species recorded (60%) were insectivores that presented the entire range in foraging heights, from the forest floor, such as *M. insularis*, *P. erythroge-nys*, Chinese Bamboo Partridges [*Bambusicola thoracicus* (Temminck, 1815)], to the medium, such as *A. albogularis*, *E. zantholeuca*, and *H. azurea*, to the upper layers, such as *D. aeneus*, *P. solaris*, and Gray-capped Pygmy Woodpeckers [*Dendrocopos canicapillus* (Blyth, 1845)]. The variability in perching height may dilute the relationship between diets and onset times of dawn singing. On

the other hand, it indicates that insectivores can and would locate prey from different heights or forest layers that are exposed to different levels of light availability, thus diets are less liable to be subjected to light constraints (Thomas *et al.*, 2006).

Our results indicate that foraging/perching heights by birds are a considerably more relevant factor in explaining the pattern and difference in dawn signing sequence among species. This ecological factor apparently determines the timing and level of light availability, but is also affected by the visual capability of birds and its effect on dawn chorus of different species can be subjected to the habitat structure. In forests with tall trees and structured vegetation, perching height may overshadow the difference in visual ability, while in forests with less-structured vegetation, lower or thinner canopy, or both, minor differences in visual ability may likely still play a crucial role.

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