Singing in the moonlight: dawn song performance of a diurnal bird varies with lunar phase

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Supplementary Material

Materials and methods

Study species and site

White-browed sparrow weavers are cooperatively breeding songbirds that live in groups consisting of a dominant breeding pair and non-breeding subordinate helpers of both sexes [1, 2]. Each group defends a territory throughout the year [1, 3], with group members roosting each night in individual woven sleeping chambers located in a single tree (or small cluster of trees) in the core area of the territory [1, 4]. The exact location from which a given male commences his dawn song production can therefore be predicted reliably, as they typically roost in a particular chamber, making targeted and repeated recordings highly feasible. Each chamber consists of a tube that is open at both ends; individuals spend the night with their head at one end (often visible from the ground) and are thus likely to detect changes in light levels.

The current study was conducted in the context of a longitudinal project which has been monitoring over 40 cooperatively breeding groups of white-browed sparrow weavers since 2007 [5,6]. All birds were fitted with a single metal ring and three colour rings for identification (under SAFRING license 1444), and records of group compositions were maintained with at least weekly visits. Specific individuals can be readily caught by flushing them from their roost chamber into a purpose-built capture net [7]. Sex is identified by bill colour in this subspecies; males exhibit black, whereas females have horn-coloured beaks [8]. Sparrow weaver social groups could be distinguished from one another as all group members foraged together, engaged in cooperative sentinelling behaviour, offspring care, weaving and in territorial defence against neighbouring groups. Group size in the population ranges from 2 to 12 [5].

The dominant bird of each sex was determined by weekly monitoring of key dominance-related behaviours as described in previous studies of this species [1, 3, 9, 10]. Specifically, dominants of either sex more frequently demonstrated within-group aggression such as the chasing and displacing of other individuals, the dominant pair regularly produced synchronised duet song together and the dominant male consistently produced solo song at dawn throughout the breeding season. Breeding takes place between September and May each year and groups may rear multiple clutches or may not attempt to breed at all during the breeding season (unpub. data). The lay dates of all eggs were determined via nest checks every 1 to 2 days.

Data collection

Dominant males consistently produce solo song at dawn during the breeding season, but subordinate males also occasionally sing [11]. To control for any differences in song performance that might be associated with dominance status, we focussed on dominant males only in this study. Dominant males were identified during the dawn chorus using their leg-ring combination, along with a distinct black dye mark (CLAIROL 'Nice 'n Easy Hair Colour', 124) applied to feathers on the lower abdomen during routine captures. Dye was applied to the tips of the feathers with care to ensure no contact with the skin, and was fully dried (to avoid subsequent ingestion) before returning the birds to their roost chambers. No skin irritation or changes in the behaviour and social interactions with conspecifics were observed following application of the dye. The dye marks were used to confirm individual identification as the low light levels at dawn can reduce the reliability of colour-ring discrimination.

All dawn observation sessions began approximately 2 h before sunrise, which is well before the earliest dawn song performance has been recorded to start in this population (unpub. data). Recordings of pre-emergence song were made from within 20 m of the roost tree, using a Sennheiser ME66 directional microphone with a K6 power module (2004 Sennheiser), and a Marantz PMD660 solid-state recorder (D&M Holdings Inc.). Avisoft-SASLab Pro 5.1.16 (R. Specht, Berlin, Germany) was used to generate spectrograms (Hamming window, FFT of 1024 points, time resolution of 5.8 ms and 50% overlap). The song repertoire is composed of syllables and phrases combined in a variable fashion (with syllables combined to form phrases or occasionally produced as single syllables), as opposed to discrete song 'types' that are produced by some species [12]. The duration of each syllable (that was not part of a phrase) or phrase (separated from the next syllable or phrase by more than 200 ms [12]), was measured manually for each recording.

Temperature (°C) and wind speed (km/h) were recorded every 10 min by a Watchdog 2700 fixed weather station (Spectrum Technologies, Inc.) located at the centre of the study site. Dawn temperature was calculated as the mean temperature over the 2 h period before sunrise (mean ± SD = 20 ± 2.5 °C; range = 15–24°C); dawn wind speed was similarly averaged for the 2 h period before sunrise (mean ± SD = 6.4 ± 5.0 km/h; range = 0.5–16.8 km/h).

The percentage of the surface area of the moon reflecting light (which was used to assign moon 'phase': 'new' = 0–35%; 'full' = 65–100%) was as reported by the USNO astronomical data service. Location-specific predicted values for the time of nautical twilight (when the sun is 12 degrees below the horizon) were obtained from the United States Naval Observatory (USNO) data service (http://www.usno.navy.mil/USNO/astronomical-applications/data-services). The order of new and full moon sessions (one of each for each focal male) was alternated between individuals in a balanced fashion, with sampling sessions distributed across six complete lunar cycles between October 2010 and April 2011.

Data analysis

For analyses of performance event times, the time of day was first converted into numeric form using the 'POSIXct' function and subsequently standardised to have a mean of 0 and standard deviation of 1 prior to model fitting [13]. For all analyses, residuals were checked for normality and homoscedasticity, and either met these assumptions or nonparametric tests were used. In all Linear Mixed Models (LMMs), the starting point was a full model and then stepwise removal of the least significant term took place until the minimal adequate model was identified (when only significant terms remained) [14]. The significance of explanatory variables was obtained by testing for the change in deviance in the fit of the model when the term was removed. 'Individual' was included as a random effect to account for repeated measures from the same male. In initial models, the only fixed term was nautical twilight time; in subsequent models, fixed terms initially included were moon phase, moon position and the interaction between the two. Significance values for nonparametric paired tests were obtained by consulting critical value tables as exact values are not provided by 'R' [15]; the alpha value was set at 0.05.

Results

Table 1. The outcomes of linear mixed effects models to investigate the role of lunar phase and position on (a) song performance start time, (b) roost emergence time, and (c) song performance end time (n=19 dominant males, 38 observations), with song event times calculated as the difference between the event time and nautical twilight that day. The p value for each term is based on the chi-square test for change in deviance when comparing models with or without that term. The mean effect estimates ± SE (effect sizes) are reported for terms retained in the minimal model. *Random terms: variance is reported.

		Minimal model		
Response	Predictors	Estimate ± SE	χ^2	P
a) Start time	Position × phase	9.68 ± 2.95	9.34	**0.0022**
	Position (Above)	-4.39 ± 6.13		
	Phase (New)	0.98 ± 2.24		
	(Intercept):	16.17 ± 4.66		
	Individual ID*:	153.99		
b) Emergence time	Position × phase		2.56	0.11
	Position		0.47	0.49
	Phase		2.44	0.12
	(Intercept):	32.02 ± 1.29		
	Individual ID*:	14.63		
c) End time	Position × phase		1.29	0.25
	Position		0.057	0.81
	Phase		0.19	0.65
	(Intercept):	44.23 ± 1.22		
	Individual ID*:	17.02		

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