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Animal behaviour

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

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It is well established that the lunar cycle can affect the behaviour of nocturnal animals, but its potential to have a similar influence on diurnal species has received less research attention. Here, we demonstrate that the dawn song of a cooperative songbird, the white-browed sparrow weaver (*Plocepasser mahali*), varies with moon phase. When the moon was above the horizon at dawn, males began singing on average 10 min earlier, if there was a full moon compared with a new moon, resulting in a 67% mean increase in performance period and greater total song output. The lack of a difference between full and new moon dawns when the moon was below the horizon suggests that the observed effects were driven by light intensity, rather than driven by other factors associated with moon phase. Effects of the lunar cycle on twilight signalling behaviour have implications for both pure and applied animal communication research.

1. Introduction

It is well known that the lunar cycle underpins reproductive synchrony in many species, particularly amphibians, fishes and marine invertebrates [1–3]. There is also strong evidence that subtle moon-related gravitational, magnetic and light fluctuations can markedly influence the communication, foraging and anti-predator behaviour of nocturnal animals, with consequences for individual fitness, interspecific interactions and community structure [1,2]. However, while the lunar cycle could, in theory, have similar effects on the behaviour of diurnal animals, especially those that are active in twilight periods, this possibility has received little direct empirical testing [4,5].

The dawn chorus of passerine birds is a classic example of the twilight peaks in sexual signalling and territorial displays that occur across a range of taxa [6]. Communication at this time of day is particularly important for mate choice and intra-sexual competition [7,8]. Characteristics of dawn song performance may therefore have evolved as honest signals of male quality. For instance, dawn chorus start time is related to age in male blue tits (*Cyanistes caeruleus*) and winter social rank predicts the dawn chorus performance duration of male black-capped chickadees (*Parus atricapillus*), with age and social rank being key determinants of reproductive success in these species [9,10]. Hence, external influences on dawn song performance have the potential to affect individual fitness [10], and environmental factors have previously been shown to be important in this regard [11–13]. However, whether the lunar cycle plays a role is unknown, to the best of our knowledge, despite the novel challenges that such temporal dynamics would pose for signallers and receivers.

Here, we investigate how two aspects of the lunar cycle—moon phase (new or full) and moon position at dawn (above or below the horizon)—affect the dawn song of a diurnal bird, the white-browed sparrow weaver (*Plocepasser mahali*). Song from a repertoire expressed only during the breeding season is produced by male sparrow weavers as a discrete daily performance at dawn [14]. Males commence

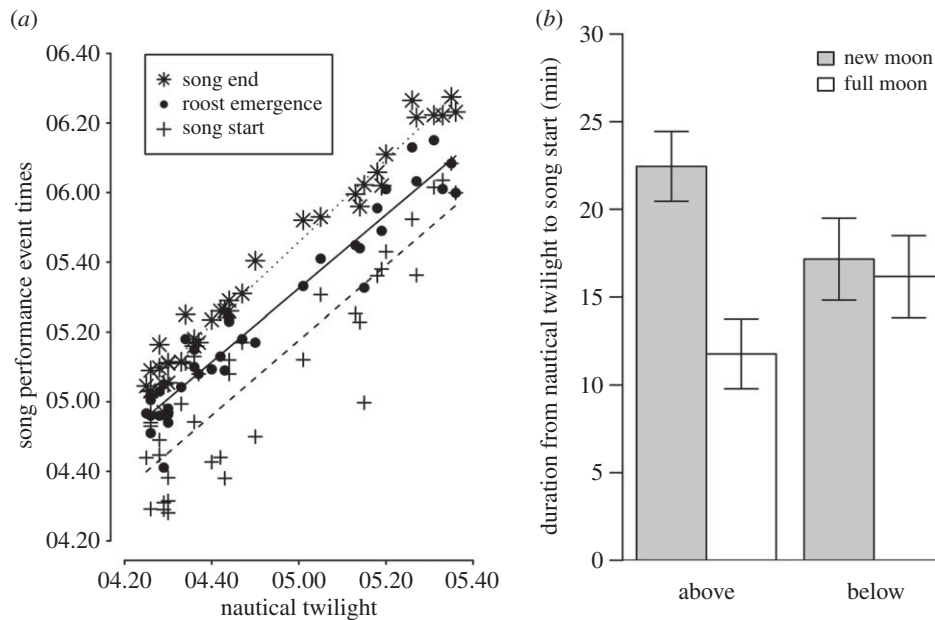


Figure 1. (a) The time of nautical twilight as a predictor for the start, emergence and end times of the dawn song performance ($n = 19$ males), with regression lines of best fit; (b) mean \pm s.e. (from LMM) duration after nautical twilight that dawn song started (moon above the horizon at dawn: $n = 11$ males; moon below the horizon at dawn: $n = 8$ males).

singing from their short, open-ended overnight roost chambers before emerging to continue their song performance around the territory. Initially, we therefore examined the effects of moon phase and position at dawn on song start time, roost emergence time and song end time. Having discovered that males start singing earlier when there is a full moon compared with a new moon, but only when the moon is above the horizon at dawn, we investigated whether males respond to the consequently longer available performance period by singing for a smaller proportion of the time or by increasing their total song output.

2. Material and methods

Data were collected between October 2010 and April 2011 from a colour-ringed population of sparrow-weavers at the Tswalu Reserve ($27^{\circ}15' S$, $22^{\circ}26' E$) in the Kalahari Desert, South Africa (see [15,16] for study population and site details). Female reproductive stage, which can influence dawn song [17], was calculated as the time between the observation session and the next egg-laying by the male's social mate. Environmental factors that could influence dawn song, such as wind speed and temperature [11], were recorded every 10 min. Full details of methods are provided in the electronic supplementary material.

Lunar cycles were classified according to moon 'position', which indicated whether the moon was above ('exposed') or below ('hidden') the horizon at dawn, and moon 'phase', which indicated the percentage of the surface area reflecting light ('new': 0–35%; 'full': 65–100%). Song start time (when the first syllable of dawn song was produced), roost emergence time (when the male left his roost chamber) and song end time (when the last syllable of dawn song was produced) were recorded, exclusively on mornings with no cloud cover, from 19 males during both a new moon dawn and the following or preceding full moon dawn (mean \pm s.d. days apart: 15.1 ± 5.2 ; range: 7–23); 11 of these males were sampled in both conditions during exposed moon dawns and eight during hidden moon dawns.

To investigate further how moon phase influences song production on exposed moon dawns, full recordings of pre-emergence song were made for six males on both full and new moon dawns; post-emergence song was not used, because

recording quality was less consistent once birds were moving around their territories. From the recordings, the combined duration of all syllables and phrases was determined, and thus the proportion of time singing and total song output were calculated.

All statistical analyses were conducted on datasets (uploaded to Dryad (Dryad data repository (York *et al.* data file) doi:10.5061/dryad.q2s0s) using R v. 3.0.1. Initially, linear mixed-effects models (LMMs; R package 'lme4'; [18]) were used to examine the influence of nautical twilight time on song start time, roost emergence time and song end time. Having found strong correlations, and in keeping with previous studies [19], times relative to nautical twilight were then analysed in LMMs to assess the importance of moon phase and position. Qualitatively, the same results were obtained if sunrise time was used rather than nautical twilight time. Paired tests were used to assess whether there were differences between exposed full moon and exposed new moon dawns in potential confounding factors (temperature, wind speed, female reproductive stage), the time available for singing (song start time until song end time; performance period), the proportion of the performance period filled with song and the total time spent singing (total song output).

3. Results

There was a significantly positive relationship between the time of nautical twilight and the timings of all three behavioural events (LMM, song start time: $\chi^2_1 = 36.62$, $p < 0.001$; roost emergence time: $\chi^2_1 = 76.37$, $p < 0.001$; song end time: $\chi^2_1 = 115.31$, $p < 0.001$; figure 1a). Song start time was significantly affected by the interaction between moon phase and moon position ($\chi^2_1 = 9.34$, $p = 0.0022$; electronic supplementary material, table S1). Males started singing earlier when there was a full moon compared with a new moon on exposed moon mornings, but there was no difference in start times between moon phases on hidden moon mornings (figure 1b). By contrast, the interaction between moon phase and moon position did not significantly affect either roost emergence time ($\chi^2_1 = 2.56$, $p = 0.11$) or song end time ($\chi^2_1 = 1.29$, $p = 0.25$); neither moon phase nor moon position had a significant main effect on either event time (see electronic supplementary material, table S1).

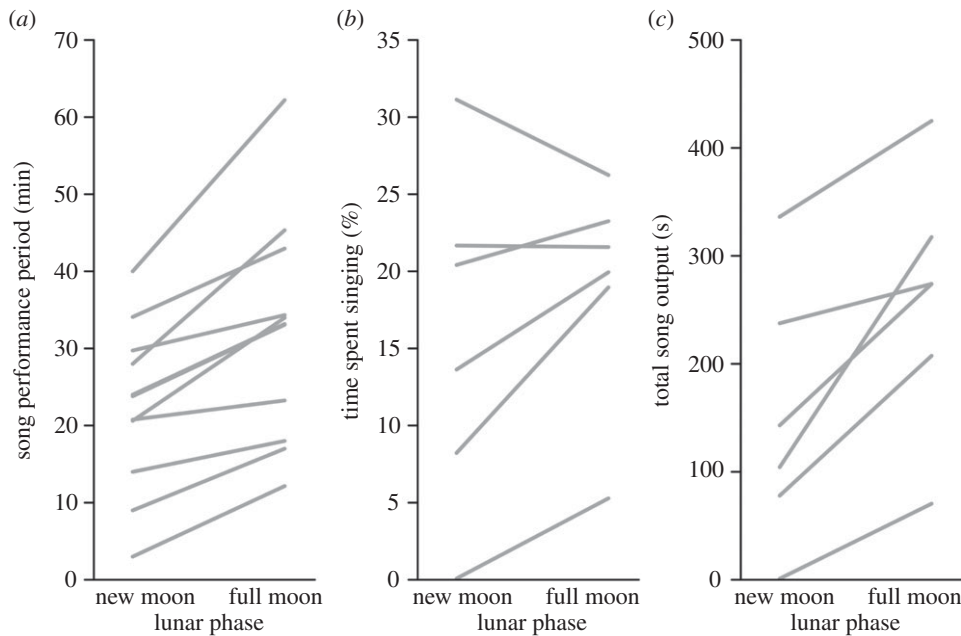


Figure 2. Differences in song characteristics between new and full moon dawns when the moon was above the horizon: (a) song performance period ($n = 11$ males); (b) percentage time spent singing ($n = 6$ males) and (c) total song output ($n = 6$ males). Shown in all cases are values for individual males, with those from the same male connected by lines.

The difference in song start time between full and new moon dawns on exposed moon mornings cannot be attributed to differences in temperature (paired t -test: $t_{10} = 0.64$, $p = 0.540$), wind speed ($t_{10} = 0.75$, $p = 0.468$) or female reproductive stage ($t_8 = 0.58$, $p = 0.580$). Given the earlier song start time, but same song end time, males therefore sang over a significantly longer performance period under full than new moons on exposed moon mornings (paired t -test: $t_{10} = 5.58$, $p < 0.001$; figure 2a). They did not compensate for this by singing for a smaller proportion of the available time (Wilcoxon test: $V = 7$, $n = 6$, $p > 0.50$; figure 2b) and, consequently, males produced significantly greater actual song output during full moon compared with new moon mornings ($V = 21$, $n = 6$, $p = 0.016$; figure 2c).

4. Discussion

Our study shows that dawn song in white-browed sparrow weavers varies with moon phase and position relative to the horizon. Males started singing earlier when the moon was full compared with when it was new, as long as the moon was above the horizon at dawn. During these exposed full moon dawns, males sang over a longer performance period and produced more song during that period compared with exposed new moon dawns. While it is well established that the lunar cycle can influence the behaviour of nocturnal animals [1–3], our results indicate its potential to have effects on the behaviour of diurnal animals, especially during twilight periods.

Males that are able to start their dawn song earlier on exposed full moon mornings could gain reproductive advantages [12], if receivers use start time as an indicator of quality [9,10], and if dawn is the key time for seeking extra-pair mates [7] or territorial vacancies [8]. For receivers, a longer performance period should provide more time to assess and compare individual signallers. Moreover, if the production of a greater song output is physically more demanding [20],

then differences in signaller quality might be more easily determined on exposed full moon mornings.

The documented differences in song performance between full and new moon dawns on exposed moon mornings cannot be readily attributed to differences in cloud cover, wind speed, temperature or female reproductive stage [11,17]. It is also unlikely that geophysical forces associated with the lunar cycle [1,21] can account for the observed differences in song, because these differences were not apparent when the moon was hidden at dawn. Differences in foraging success the day before, potentially owing to lunar-related fluctuations of activity in nocturnal or crepuscular insects, might be another causal factor; this possibility would require future investigation. However, the most likely explanation for our observations is a difference in illumination levels between new and full moon dawns when the moon is above the horizon; song-related behaviours in this species are strongly affected by light levels, as evidenced by the relationship with nautical twilight time.

Lunar-related variation in dawn illumination provides a credible explanation for our findings because light levels can modulate the risk and efficiency of a variety of behaviours [6,22]. For example, as singing can divulge the location of the signaller, dawn song may typically start once predators can be detected visually [6,22], with performance start times being determined more by threshold light levels (which may be met early on exposed full moon dawns) than by fixed temporal offsets from sunrise [23]. Similarly, as dawn proceeds and light levels rise sufficiently to facilitate efficient food-finding, males may make the transition from singing to foraging [24]. The lack of an influence of moon phase on song end time may therefore reflect the minimal contribution of lunar illumination to the total environmental light levels as sunrise approaches. Further work is now needed to confirm the role of moonlight, and to assess the roles of absolute light levels at dawn or cumulative light exposure prior to sunrise or even over previous dawns [2].

Recent studies have shown that artificial lighting can lead to male passerines beginning their dawn song earlier, with a resulting reproductive benefit [12,13]. The fitness consequences

observed, which can occur at very low light levels within the range provided by full moon illumination [13], could be generated by the disruption of advertisement behaviours that are highly sensitive to light intensity [12,13]. Our findings raise the novel possibility that such sensitivity may, at least in part, have evolved in response to the regular fluctuations in light intensity at twilight that are driven by the lunar cycle.

In summary, our study indicates that acoustic signalling by diurnal animals during twilight can vary in relation to the lunar cycle; it is possible that a range of behaviours could be similarly affected. Because different species have evolved song tactics that mitigate acoustic interference from heterospecifics during the dawn chorus [6], understanding the effect of the lunar cycle on signalling dynamics at the community

level represents a challenge for future studies. More generally, we suggest that lunar phase should be considered and controlled for in studies investigating signalling behaviour during twilight, with respect to both pure behavioural questions, and when using acoustic signalling to monitor populations or assess the effects of anthropogenic change.

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