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# Female conspecifics restore rhythmic singing behaviour in arrhythmic male zebra finches

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The present study investigated whether pairing with a conspecific female would restore rhythmicity in the singing behaviour of arrhythmic male songbirds. We recorded the singing and, as the circadian response indicator, monitored the activity–rest pattern in male zebra finches (*Taeniopygia guttata*) housed without or with a conspecific female under 12 h light: 12 h darkness (12L:12D) or constant bright light (LL<sub>bright</sub>). Both unpaired and paired birds exhibited a significant daily rhythm in the singing and activity behaviour, but paired birds, under 12L:12D, showed a ~2 h extension in the evening. Exposure to LL<sub>bright</sub> decayed rhythmicity, but the female presence restored rhythmic patterns without affecting the 24 h song output. In the acoustic features, we found a significant difference in the motif duration between unpaired and paired male songs. Overall, these results demonstrated for the first time the role of the female in restoring the circadian phenotype of singing behaviour in male songbirds with disrupted circadian functions, although how interaction between sexes affects the circadian timing of male singing is not understood yet. It is suggested that social cues rendered by a conspecific female could improve the circadian performance by restoring rhythmicity in the biological functions of the cohabiting arrhythmic male partner.

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## 1. Introduction

Organisms maximize their fitness by synchronizing their physiology and behaviour with the abiotic and biotic features of their environments. This is achieved by endogenous circadian clocks, which in interaction with prevailing light, food and social environments, determine temporal patterns of events during the day in a wide array of daily functions, viz. daily activity–rest, sleep–wake and feeding patterns (Aschoff 1981). Diurnal animals are active and feed during the day and sleep at night; the converse is true of nocturnal species. However, an individual shows its internal time and exhibits rhythms in its biological functions with periods matching with that of the circadian oscillations under constant light or darkness (LL or DD; Aschoff 1981).

Bird song is a reproduction-linked trait evolved through sexual selection and closely associated with breeding success (Nowicki and Searcy 2004). Although generally only

male birds sing, the role of females in determining male singing has been documented by comparing both the song and singing behaviour of unpaired and paired male songbirds. Unpaired males tend to sing at higher rates than the paired ones in species such as great tits (*Parus major*) (Krebs *et al.* 1981), European starlings (*Sturnus vulgaris*) (Cuthill and Hindmarsh 1985) and nightingales (*Luscinia megarhynchos*) (Roth *et al.* 2009). In general, the song repertoire is larger in the unpaired than in the paired male, perhaps in order to better advertise itself to a prospective mate (Holveck and Riebel 2007). Also, unpaired males' songs may contain specific acoustic features that are more attractive to a female. Bachelor rufous-and-white wrens (*Thryothorus rufalbus*) sing with broader frequency range and syllabically more complex songs at a higher rate output as compared with paired wrens (Henkin *et al.* 2009). How pairing decreases singing is unclear, but perhaps the presence of a mate reduces the male's motivation to sing (Dunn

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and Zann 1996). A significantly reduced rate of singing in a male paired newly, as compared with a male with a bonded female partner, supports this (Dunn and Zann 1996).

Increasing evidence shows the role of social cues from a conspecific as the *zeitgeber* for circadian rhythms (see reviews by Mistlberger and Skene 2004; Favreau *et al.* 2009). The role of social cues in the synchronization of daily singing behaviour is not well understood, although similar to locomotor activity, both calling and singing behaviour are reported to be controlled by the circadian clock (Derégnaucourt *et al.* 2012; Wang *et al.* 2012). The removal of the pineal gland, one of the central circadian clocks (Kumar *et al.* 2004), and/or periodic melatonin application, has been shown to affect the pattern of singing behaviour and/or song control nuclei in house sparrows (*Passer domesticus*) (Cassone *et al.* 2008), zebra finches (*Taeniopygia guttata*) (Derégnaucourt *et al.* 2012; Wang *et al.* 2012) and Indian weaverbirds (*Ploceus philippinus*) (Surbhi *et al.* 2015).

In this study, we hypothesized that a female conspecific would synchronize the circadian-clock-governed singing behaviour to the time-of-day in male songbirds. We tested this by examining the circadian nature of singing behaviour and investigating whether pairing with a conspecific female would restore circadian phenotype of singing behaviour in males with disrupted circadian rhythms. To address these issues, we carried out experiments with zebra finches (*Taeniopygia guttata*) as their song pattern is well characterized and the underlying mechanisms are relatively understood (Nottebohm *et al.* 1990; Dunn and Zann 1997). We recorded singing patterns and, as the circadian response indicator, monitored daily activity–rest pattern in male zebra finches housed without and with a conspecific female under 12 h light: 12 h darkness (12L:12D) or constant (24 h) bright light (LL<sub>bright</sub>). LL<sub>bright</sub> causes disruption of circadian rhythms in activity behaviour in several songbirds including zebra finches (McMillan *et al.* 1975; Cassone *et al.* 2008; Wang *et al.* 2012; Surbhi *et al.* 2015).

## 2. Materials and methods

This study was conducted on adult zebra finches (*Taeniopygia guttata*), with the approval of the Institutional Animal Ethics Committee of the Department of Zoology, University of Delhi, India. The adult male birds taken out from the breeding colony were randomly separated into two groups (n=7 each), and singly housed in activity-cum-song recording cages (42×30×54 cm) that were individually placed in the light-tight wooden boxes (58×52×68 cm). These boxes, maintained at constant temperature (22±2°C), provided 12 h light: 12 h darkness (12L:12D; L=100 lux at cage floor level, D=0 lux). Food (*Setaria italica* seeds) and water were provided *ad libitum*. After a week of 12L:12D, a female conspecific from the same breeding colony was

introduced in each cage housing the group 1 finches and then the ‘pairs’ were maintained under 12L:12D for another week. At the same time, the group 2 birds were released in constant light by extending the daylight into 12 h night (LL<sub>bright</sub>, 100 lux at cage floor level) to abolish the daily (circadian) rhythm in the daily activity–rest pattern established under 12L:12D. After a week of LL<sub>bright</sub>, each cage was introduced with a female conspecific as in group 1, and then the ‘pairs’ were maintained under LL<sub>bright</sub> for another week. Thus, each male was unpaired and paired for an equal length of time (1 week) under both 12L:12D and LL<sub>bright</sub> conditions. The activity–rest pattern emanating from each cage was continuously monitored, which served as the internal circadian clock response indicator (Daan and Aschoff 1975). Sound (singing) was recorded consecutively over the last 2 days of the unpaired and paired conditions. Additionally, the activity–rest pattern of seven females under 12L:12D was monitored in order to show that they exhibit activity behaviour similar to males, although unlike males, they do not sing (Bottjer *et al.* 1985).

### 2.1 Measurement of activity–rest and song patterns

A passive infra-red sensor (digital PIR motion detector, LC-100-PI) mounted on the cage was used to continuously monitor the general activity of each bird, and it transmitted in 5 min bins to a channel of the computerized Data Quest system, as has been previously described (Malik *et al.* 2004; Singh *et al.* 2010). The collection, graphics and analysis of activity were done by ‘The Chronobiology Kit’ software program of Stanford Software Systems, Stanford, USA. Double-plotted activity records wherein successive days’ activity was plotted sideways and underneath, for the entire duration of an experiment, was obtained; this actogram was considered the signature graphic of an individual.

Similarly, each box was fitted with a Behringer C-2 Studio condenser microphone to record the calls and songs using M-Audio Profire 2626 8-channel Sound Card and Nuendo Application software from Steinberg Media Technologies GmbH, Germany. Basically, it recorded sound at 16-bit rate and 44.1 kHz sampling frequency, which was stored as digital audio files in the AVI format. An entire song file of 48 h of song recordings was manually screened for identifying and analysing song bouts of each individual. Typically, a song bout consists of motifs strung together lasting 2–7 s (Saar and Mitra 2008). A silence gap of ≥2 s was considered as two separate song bouts. For each individual, we first calculated the average number of song bouts for each hour of the day, and from this a 24 h song-profile was generated for each group in each light condition. Also, 30 bouts from the same 48 h recordings were randomly selected and used to calculate the duration of a song bout and the number of motifs per song bout.

2.1.1 *Analysis of a song motif*: A motif, considered as the functional unit of zebra finch song (Zann 1996), is an assemblage of syllables that are repeated in an almost fixed pattern (Williams 2004), albeit with minor variations (Williams and Mehta 1999). We analysed song motifs using the Explore and Score module of Sound Analysis Pro 2011 software (SAP 2011; [http://ofer.sci.ccny.cuny.edu/\\_sound\\_analysis\\_pro](http://ofer.sci.ccny.cuny.edu/_sound_analysis_pro)). By adjusting the Weiner entropy and amplitude thresholds, we selected 30 song bouts from the same time of the day for both unpaired and paired conditions; specifically, we picked song bouts during 1 h in the morning (0900–1000), and selected the first motif of the bout. This was done so as to avoid the effects of changes, if any, in the acoustic features of song motifs over the course of a single bout (Chi and Margoliash 2001) and over the course of a day (Aronov and Fee 2012). Finally, various acoustic features of a song motif, viz. the duration, amplitude and amplitude modulation, pitch, frequency and frequency modulation, and Weiner entropy were calculated to determine the effects of social and light conditions.

## 2.2 Statistics

All values are presented as mean ( $\pm$ SEM). Statistical analyses were performed by GraphPad Prism version 5.0 (La Jolla, CA, USA). One-way analysis of variance with repeated measures (one-way RM ANOVA) followed by the Newman-Keuls *post hoc* test was used to obtain the significance variations in the activity and singing behaviours over 24 h in each experimental condition. Thereafter, an analysis tested the circadian rhythm in respective conditions based on unimodal cosinor regression  $y=A + [B \cos(2\pi(x-C)/24)]$  (A, B and C are the mesor (mean value), amplitude and acrophase of the rhythm, respectively). The significance of regression analysis was calculated by using the number of samples,  $R^2$  values and numbers of predictors (mesor, amplitude and phase; Soper 2013, <http://www.danielsoper.com/statecalc3/calc.aspx?id=15>). Chi-square periodogram analysis determined the circadian period of a rhythmic behaviour. Two-way with or without repeated measures (two-way ANOVA or two-way RM ANOVA) and Bonferroni post-test was used to determine the effects of two factors (unpaired/paired, 12L:12D/LL<sub>bright</sub>, or time-of-day) and their interaction on a study parameter. Wilcoxon matched-pairs signed rank test was used to analyse the differences in the motif duration. Finally, Rayleigh's test was used to determine uniformity in distribution of activity and singing behaviour, and Watson's  $U^2$  test was used to determine differences in the behavioural pattern between the LD and LL<sub>bright</sub> conditions (Bayne and Hobson 1997). Significance was considered at  $p<0.05$ .

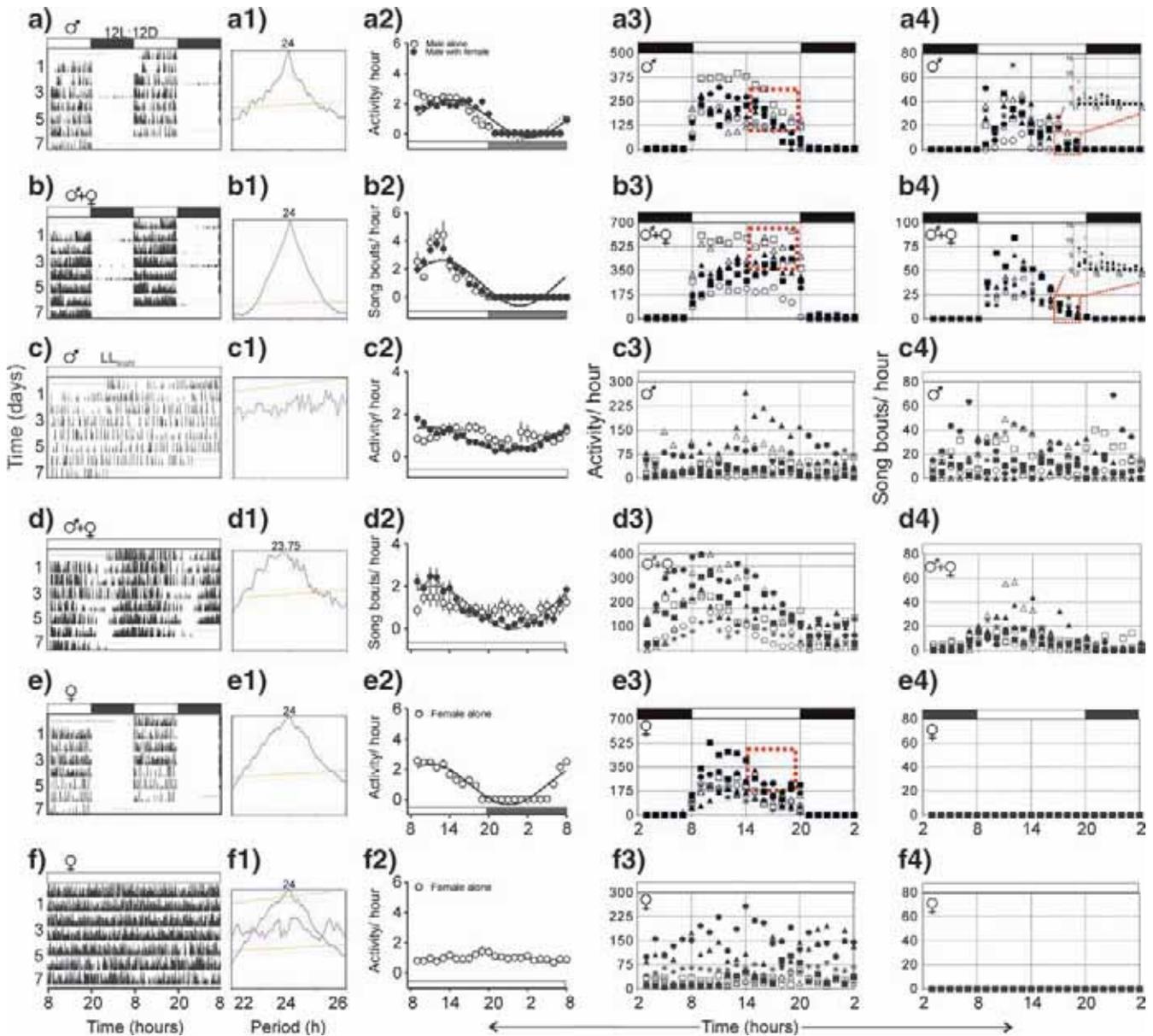
## 3. Results

### 3.1 Effects on daily activity and singing behaviours under 12L:12D

All male birds exhibited a diurnal pattern with significant variation in their activity and singing behaviours under 12L:12D (activity:  $F_{23,138}=34.10$ ,  $p<0.001$ ; singing:  $F_{23,138}=17.38$ ,  $p<0.001$ ; one-way RM ANOVA; figure 1a–a4). Cosinor analysis revealed that both behavioural patterns conformed to a significant daily rhythm (activity:  $p<0.001$ ,  $F=116.33$ ; singing:  $p<0.001$ ,  $F=39.26$ ; figure 1a2 and b2) with the LD cycle synchronized period of  $\tau=24$  h (figure 1a1). Daily activity pattern was similar in both male and female finches (figure 1a–a3, e–e3). Introduction of a female in the male's cage did not alter the emanating activity and singing patterns (figure 1a–a4, 1b–b4). That is, birds continued to show significant daily variations (activity:  $F_{23,138}=40.24$ ,  $p<0.001$ ; singing:  $F_{23,138}=28.24$ ,  $p<0.001$ ; one-way RM ANOVA; figure 1b2–b4) with a significant rhythm (cosinor analysis – activity:  $p<0.001$ ,  $F=121.45$ ; singing:  $p<0.001$ ,  $F=83.10$ ; figure 1a2 and b2) in both the activities synchronized with the 12L:12D ( $\tau=24$  h; figure 1b1). Although, after pairing, the activity levels were almost doubled, as expected for two individuals in the cage, the duration of both activity and singing was most strikingly extended and elevated in the evening 2 h of the 12 h light period. There was an effect of the social condition, i.e. female presence (activity:  $F_{1,24}=23.98$ ,  $p<0.001$ ; singing:  $F_{1,132}=5.86$ ,  $p<0.05$ ), time-of-day (activity:  $F_{2,24}=9.17$ ,  $p<0.001$ ; singing:  $F_{11,132}=7.57$ ,  $p<0.001$ ) and condition  $\times$  time-of-day interaction (activity:  $F_{2,24}=7.45$ ,  $p<0.05$ ; singing:  $F_{11,132}=1.473$ ,  $p=0.15$ ) during the evening 3 h of the 12L:12D condition (figure 1a3, a4, b3, b4; two-way RM ANOVA). But, when considered for the entire day, two-way RM ANOVA revealed a significant effect of the time-of-day ( $F_{23,138}=44.37$ ,  $p<0.001$ ) and condition  $\times$  time-of-day interaction ( $F_{23,276}=2.09$ ,  $p<0.05$ ), not the social condition (female presence:  $F_{1,276}=4.22$ ,  $p=0.062$ ), on male singing behaviour under 12L:12D (figure 1b2).

### 3.2 Effects on daily activity and singing behaviours under LL<sub>bright</sub>

LL<sub>bright</sub> abolished the diurnal pattern of activity ( $F_{23,115}=0.84$ ,  $p=0.67$ ) and singing ( $F_{23,138}=0.63$ ,  $p=0.89$ ; one-way RM ANOVA; figure 1c3 and c4) and caused decay of rhythmicity in the activity ( $p=0.07$ ,  $F=2.30$ ) and singing ( $p=0.12$ ,  $F=1.98$ ) behaviour of group 2 birds (cosinor analysis; figure 1c2 and d2). Chi-square periodogram analysis validated the loss of activity rhythm in 6 out of 7 individuals under LL<sub>bright</sub> condition. Data from one bird that was not fully



**Figure 1.** Representative actogram of a male zebra finches *Taeniopygia guttata* (a–d) when housed (a) alone with 12 h light: 12 h darkness (12L:12D), when (c) alone with constant bright light (LL<sub>bright</sub>), when housed with a female (b) with 12 h light: 12 h darkness (12L:12D), and when housed with a female (d) with constant bright light (LL<sub>bright</sub>). (e–f) Similar representative actogram of a female zebra finch housed single (e) with 12L:12D and (f) with constant bright light (LL<sub>bright</sub>). (a1–f1) Period of activity rhythm, as determined by Chi-square periodogram. (a2–f2) Hourly profile over 24 h of activity and male singing behaviour in zebra finches (mean±SEM; n=6 or 7) under respective conditions, and the curve passing through hourly values indicates the shape of the rhythm, as determined by cosinor analysis. (a3–e4) Scatter plot of hourly activity and male singing behaviour in each condition, with boxes showing the enhanced period of activity, and inset graphs show detailed profile in 15 min bins during the evening 3 h light period. Horizontal bars indicate the light (open) and dark (closed) periods, as appropriate. (a2–f2) plot average values, whereas (a3–f3) and (a4–f4) plot individual values in a group; each individual is shown by different symbols.

arrhythmic in activity during 1 week of LL<sub>bright</sub> was excluded from further analysis. The presence of a female restored a significant rhythm in the activity ( $F=33.52$ ,  $p<0.001$ ;

figure 1c2) and male singing ( $F=30.32$ ,  $p<0.001$ ; figure 1d2; cosinor analysis) behaviours. Both activity and singing exhibited significant daily variations (activity:

$F_{23,115}=8.168$ ,  $p<0.001$ ; singing:  $p<0.001$ ,  $F_{23,138}=5.75$ ; figure 1d3 and d4) and were temporally phased with an average  $\tau$  of  $23.9\pm 0.08$  h and  $24.6\pm 0.44$  h for activity and singing, respectively (figure 1d1 and d2). Two-way RM ANOVA revealed a significant effect of the social condition (female presence:  $F_{1,276}=4.99$ ,  $p=0.045$ ) and time-of-day ( $F_{23,276}=2.96$ ,  $p<0.001$ ) but not of the condition  $\times$  time interaction ( $F_{23,276}=0.73$ ,  $p=0.81$ ) on male singing behaviour under  $LL_{\text{bright}}$  (figure 1d2). However, daily song bouts were not affected (figure 3f). Female zebra finches also became arrhythmic in activity behaviour under  $LL_{\text{bright}}$  condition (figure 1f1–f4). Rayleigh's test further revealed that activity and singing patterns were not uniformly distributed ( $p<0.05$ ) in both the LD (activity: figure 2a1 and a2; singing: figure 2b1 and b2) and  $LL_{\text{bright}}$  conditions (activity: figure 2c1 and c2; singing: figure 2d1 and d2). Also, activity and singing were higher in LD than in  $LL_{\text{bright}}$  in both social conditions of male alone vs. male in pair (activity: female absence  $U^2=3.55$ ,  $p<0.001$ ; female presence  $U^2=2.97$ ,  $p<0.001$ ; singing: female absence  $U^2=1.84$ ,  $p<0.001$ ; female presence  $U^2=2.84$ ,  $p<0.001$ ; Watson's  $U^2$  test).

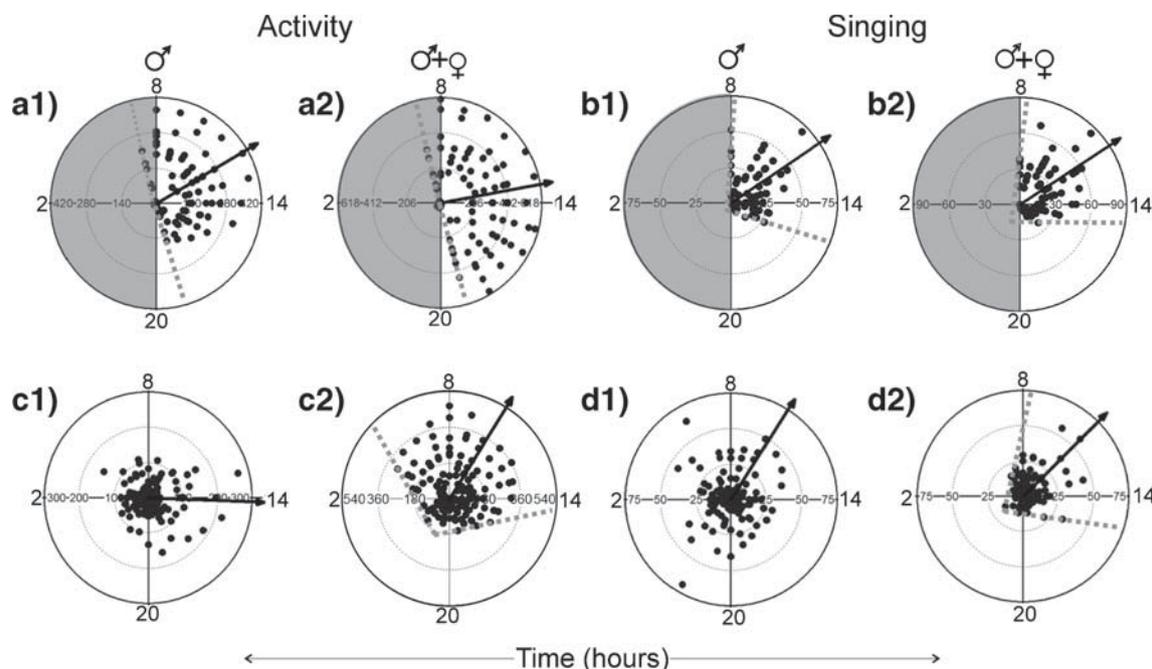
### 3.3 Effects on male song features

The duration of a song motif differed between the social conditions under  $LL_{\text{bright}}$ , with a significantly longer motif in

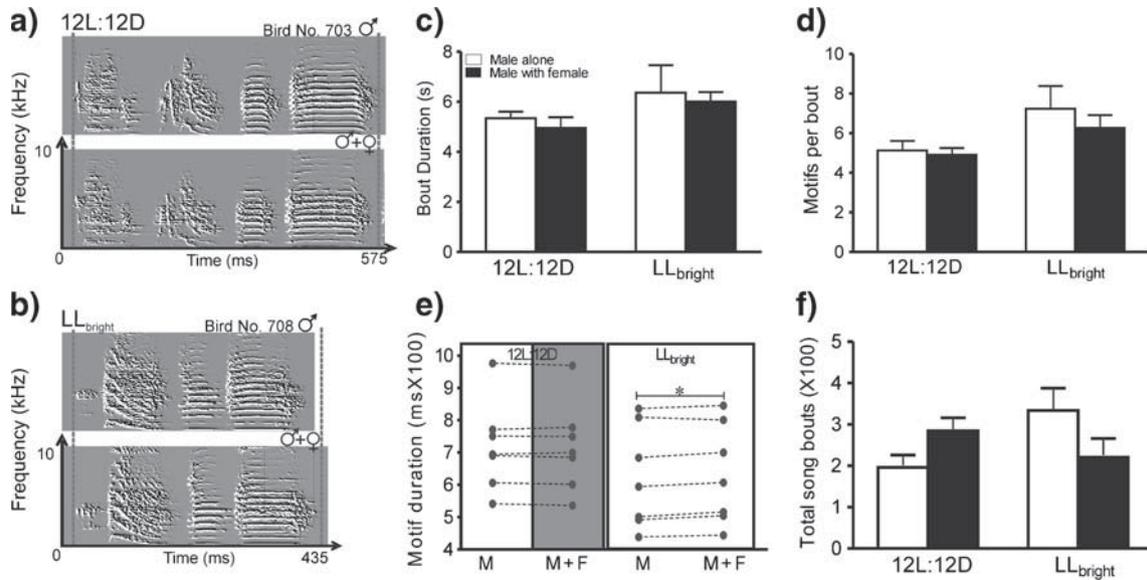
the paired male than the unpaired male (Wilcoxon matched-pairs signed rank test,  $p=0.046$ ; figure 3b and e). However, there was no effect of either social or light condition on the duration of a song bout or motifs per song bout (figure 3c and d). Table 1 compares the spectral features of a song motif between unpaired and paired males. Clearly, there were no differences in the spectral features between the two social conditions. Two-way RM ANOVA revealed no significant effect of social condition or of light condition on the acoustic features measured, viz. amplitude and amplitude modulation, pitch, frequency and frequency modulation, and Wiener entropy (table 1).

## 4. Discussion

Results show that in correspondence with the activity rhythm, male zebra finches exhibited a synchronized daily rhythm in singing under 12L:12D. Both rhythms decayed under  $LL_{\text{bright}}$  but were restored after the introduction of the female (figure 1d2). We conclude that (i) circadian rhythm determines daily timing of male singing, as is also suggested by previous studies (Derégnaucourt *et al.* 2012; Wang *et al.* 2012), and (ii) social cues rendered by a female conspecific can serve as the *zeitgeber* for both the circadian activity and singing behaviour in male zebra finches (figure 1c2). The restoration of rhythmicity in the paired condition took 4–5



**Figure 2.** Polar scatter plots of activity and singing behaviour of male zebra finches (*Taeniopygia guttata*;  $n=7$  each) when housed alone (a1–d1) and when housed with a female (a2–d2) under 12 h light: 12 h darkness (12L:12D, upper panel) or constant bright light ( $LL_{\text{bright}}$ , lower panel). Each point in the circle represents an individual value and solid arrows indicate the weighted mean for all the values. Broken lines indicate the limit of activity and singing spread over 24 h. Open and shaded areas represent the light and dark periods, respectively.



**Figure 3.** Sonograms and acoustic features of male zebra finches (*Taeniopygia guttata*) when housed alone (upper panel or open bars) and when housed with a female (lower panel or closed bars). (a, b) Representative sonogram of a male bird under 12 h light: 12 h darkness (a) or constant bright light (b). (c, d, f) Mean ( $\pm$ SEM) duration of a song bout (c), motifs per song bout (d) and total song bouts over 24 h (f) in two social and light condition, as above. (e) Individual plots of the duration of song motif of birds in both social conditions (male alone or male with female) under 12L:12D and constant bright light (LL<sub>bright</sub>). \* indicates significant difference between male and male + female at  $p < 0.05$  level (Wilcoxon -signed rank test).

days under LL<sub>bright</sub>, possibly due to time taken in establishing the mutual social interaction in two sexes. These results are consistent with the idea of mutual synchronization of circadian functions, as suggested by studies in the house sparrows (*Passer domesticus*) (Menaker and Eskin 1966), bat (*Hipposideros speoris*) (Marimuthu *et al.* 1981) and deer mice (*Peromyscus maniculatus*) (Crowley and Bovet 1980). Daily timed presentation of a social stimulus is shown to entrain circadian activity behaviour in several species including the fruit fly (*Drosophila melanogaster*) (Levine *et al.* 2002), killfish (*Fundulus heteroclitus*) (Kavaliers 1980), free-living beaver (*Castor canadensis*) (Potvin and Bovet 1975), bat (*Hipposideros speoris*) (Marimuthu *et al.* 1981), Syrian hamster (*Mesocricetus auratus*) (Mrosovsky 1988), diurnal rodent (*Octodon degus*) (Goel and Lee 1995) and snow root vole (*Microtus oeconomus*) (Korslund 2006).

Interaction with a conspecific can confer adaptive advantages, such as to survive better through a challenging situation faced in the environment (Jullien and Clobert 2000). For example, the presence of a conspecific rendered survival advantage to migratory redheaded buntings (*Emberiza bruniceps*) subjected to a challenged feeding environment created through restricted food availability periods (Singh *et al.* 2010). Similarly, house sparrows in a larger group acquired better innovative problem-solving skills (Liker and Bókony 2009). Also, Gautier *et al.* (2008) found modulated expression of the carotenoid-based sexual signal in

males in the presence of female zebra finches. Here, the duration of both activity and singing was extended by about 2 h as a result of conspecific female presence (figure 1a4 and b4), consistent with evidence for social cues inducing physical activity in nocturnal rodents (Goel and Lee 1995). Enhanced activity is perhaps because of the maximum opportunity for communication between the paired conspecifics. Intriguingly, however, paired conspecifics also share their space and food resources, which may be a critical variable for temporal phasing of daily behaviours (Mistlberger and Skene 2004). Further, the presence of a social mate did not affect daily song output, inconsistent with the idea of social facilitation or suppression of singing in male zebra finches (Caryl 1981; Dunn and Zann 1997; Jesse and Riebel 2012). We assume that, for most part, male singing was of undirected nature, since the directed songs make up a very small fraction of the daily song output in zebra finches (Dunn and Zann 1996). In fact, in zebra finches, a novel female mate elicits directed songs for only a very brief period of time (Riebel 2009), and this rapidly declines during a longer cohabitation period (Dunn and Zann 1997). We cannot not rule out pair formation but would argue that the 1 week cohabitation period in this study was perhaps too short to establish them as the reproducing pair. Furthermore, there were no significant effects of female presence on acoustic features of the song under both 12L:12D and LL<sub>bright</sub> conditions (table 1). At this time, we

**Table 1.** Spectral features of a song motif of male zebra finches (n=14) (mean±SE) under 12L:12D and LL<sub>bright</sub> when the males were alone or when they were with a female

Acoustic features	Light condition			
	12L:12D		LL <sub>bright</sub>	
	Social condition		Social condition	
	Male alone	Male with female	Male alone	Male with female
Mean amplitude (dB)	46±0.9	46±0.8	47±1.0	47±1.0
Mean pitch (Hz)	1090±77	1121±86	1280±171	1266±148
Mean FM	38±0.9	37±1.1	38±1.2	35±1.7
Mean AM (×10 <sup>-4</sup> )	594±71	634±26	584 ±70	585±64
Mean entropy	-2.62±0.1	-2.63±0.1	-2.50 ±0.2	-2.75±0.2
Mean goodness	238±21	244±20	236±22	275±23
Mean mean frequency (Hz)	4016±107	3953±104	4054±103	3879±92
Variance amplitude (dB)	7.8±0.2	8.05±0.3	7.9±0.6	8.1±0.4
Variance pitch (kHz)	2179±99	2109±101	2199±151	1877±139
Variance FM	569±15	589±17	565±18	597±15
Variance AM (×10 <sup>-4</sup> )	189±11	191±11	185±10	168±11
Variance entropy	0.62±0.04	0.64±0.05	0.68±0.06	0.68±0.07
Variance goodness	172±23	181±20	172±23	198±22
Variance mean frequency (kHz)	435±78	424±58	421±85	399±77

cannot not rule out that this was due to the time lag that occurred in recording the song, which was done after a week of female introduction – 1 week of female exposure may have compromised the novelty factor. The effect of the female on song features has been usually measured within a few first days of its introduction into the male's cage (Atagan and Forstmeier 2012; Jesse and Riebel 2012). In the present study, nonetheless, the duration of song motifs was found significantly increased under LL<sub>bright</sub> in males housed with females. This is inconsistent with a previous finding in which a 2 week LL-exposure decreased the motif duration in zebra finches (Derégnaucourt *et al.* 2012). It was argued that LL-induced decline in acoustic features of song motifs was possibly due to suppressed daily melatonin rhythm under LL<sub>bright</sub>, because melatonin is involved in the control of the timing of motor behavioural sequences (Derégnaucourt *et al.* 2012). For the present results, we speculate that the female presence compensated for the LL-induced suppressive effects, if any, on song motifs in male zebra finches. Indeed, the presence of a conspecific can alter the circadian performance and improve overall survivorship, especially in species that live in groups. In a study carried out on male migratory redheaded buntings (referred above), Singh *et al.* (2010) have shown that the presence of a conspecific male within the cage influenced daily activity–rest pattern, maintained the body mass and reduced the mortality of males, as compared with those that lived alone.

How pairing synchronizes circadian rhythm or restores circadian phenotype in arrhythmic individuals cannot be known by this study, but we speculate that the interaction between conspecifics mutually influences the circadian timing. A study has shown that the experience gained from housing with other conspecifics can reset circadian rhythms involving the chemosensory mechanisms in *Drosophila* (Levine *et al.* 2002). We may caution, though, against completely ruling out the possibility that mutual masking effects could have contributed to the restoration of circadian pattern in arrhythmic male zebra finches. Overall, this study demonstrates for the first time that the presence of a female conspecific restores circadian phenotype of singing behaviour in male zebra finches with disrupted circadian functions. It is suggested in a wider sense that the social cues rendered by a conspecific female could improve the circadian performance by restoring rhythmicity in biological functions of the cohabiting arrhythmic male partner.

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