Effects of artificial light at night and male calling on movement patterns and mate location in field crickets

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Anthropogenic factors, such as artificial light at night (ALAN), are increasingly linked to significant modifications in animal behaviours, such as foraging or migration. However, few studies have investigated directly whether the presence of ALAN affects the ability to find a mate (mate location). One direct effect of the presence of ALAN is that it can create a light barrier in an otherwise dark environment. This may have significant behavioural implications for nocturnally active species if it affects their ability to respond to potential mates. Our study, using the acoustically orienting Australian black field cricket, *Teleogryllus commodus*, determined experimentally whether the presence of a fragmented light environment influenced movement patterns of virgin females and males. Moreover, given the importance of male song for reproductive outcomes in this species, we assessed simultaneously whether such behaviours were modified by the presence of a male attraction call. We found that while initiation of movement was slower in the presence of ALAN, the behavioural shifts associated with its presence were relatively small compared to the influence of a broadcast male attraction call. The response to the male attraction call was typically stronger for females than for males, but both males and females modified aspects of behaviour when it was present regardless of whether their immediate environment was fragmented by artificial light at night or not. Artificial light at night may alter subtle aspects of movement and mating behaviour in this species, but ultimately does not provide a barrier to movement or mate location.

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Artificial light at night (ALAN) is a potent and globally widespread urban pollutant (Kyba et al., 2017; Longcore & Rich, 2004). The daily presence of ALAN from anthropogenic sources such as streetlights and buildings potentially masks natural patterns of light (Gaston, Duffy, Gaston, Bennie, & Davies, 2014). In animals, this can disrupt biological timings (Gaston, Davies, Nedelec, & Holt, 2017), such as the daily sleep–wake cycle (Raap, Pinxten, & Eens, 2016) or foraging behaviour (Dwyer, Bearhop, Campbell, & Bryant, 2013; Willmott, Henneken, Selleck, & Jones, 2018), but it can also have an impact on annual biological patterns such as the onset of breeding in seasonal species (Baker & Richardson, 2006; Gaston et al., 2017; Robert, Lescu, Partecke, & Chambers, 2015). Increasingly demonstrated is the negative impact of ALAN for courtship and mating behaviours, particularly in invertebrates (Botha, Jones, & Hopkins, 2017; McLay, Nagarajan-Radha, Green, & Jones, 2018; Van Geffen, Groot et al., 2015; Van Geffen, Van Eck et al., 2015).

For many sexually reproducing animals, a successful mating requires that individuals of the opposite sex are able to locate one another (Andersson, 1994). Initial location can require long-range attraction, which may be achieved through different signal modalities (e.g. visual, chemical or acoustic; reviewed by Laidre & Johnstone, 2013). For nocturnal species, chemical or acoustic cues are commonly used as the primary mode of attraction. However, in the presence of ALAN, both signal production and the capacity of receivers to perceive such cues may be disrupted. For example, in the noctuid moth *Mamestra brassicae*, exposure to ALAN during juvenile growth both reduced the amount of female sex pheromone produced and altered the composition of the pheromone blend (Van Geffen, Groot et al., 2015). Furthermore, in the geometrid moth *Operophtera brumata*, an experimental field study revealed that the presence of ALAN was correlated with a reduction in the number of mated females at a site and the number of males attracted to the female sex pheromone (Van Geffen, Van Eck et al., 2015).

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The effect of ALAN on acoustic communication is less well studied from the viewpoint of animal movement patterns. In the green frog, *Lithobates clamitans*, ALAN is linked to a reduction in male calling behaviour and an associated increase in male movement at a site (Baker & Richardson, 2006). Whether the presence of ALAN similarly affects female behaviour in *L. clamitans* was untested, but it is potentially important as they actively search for calling males. To reach an advertising male, a female typically traverses across the environment, risking predation and environmental hazards (such as increased temperature, chemical pollutants and light). The fitness benefits are clear, but they are most likely traded against potential fitness costs, which may be exacerbated if ALAN increases predation risk from visual predators (Heiling, 1999; Perry, Buchanan, Fisher, Salmon, & Wise, 2008).

Artificial light at night inevitably increases the overall brightness of the nocturnal environment, but it also potentially fragments it, creating patches (or corridors) of light through areas that would otherwise be in relative darkness. The direct effect of light-related fragmentation of the environment on nocturnal animal behaviour is currently less well understood. One potential consequence is that ALAN creates a barrier that nocturnal animals will either not cross or will be reluctant to cross (Mathews et al., 2015; Stone, Jones, & Harris, 2009). However, for species that are attracted to light, ALAN could also act as an ecological trap drawing an animal into a suboptimal environment (Hale & Swearer, 2016; Macgregor, Evans, Fox, & Pocock, 2017; McLaren et al., 2018). The fitness implications for both scenarios are arguably more serious if the resulting fragmentation of the landscape impedes, either directly or indirectly, future mating opportunities.

Here, we tested experimentally whether the presence of a light-fragmented environment affected movement patterns and precopulatory mating behaviour in male and female Australian black field crickets, *Teleogryllus commodus* Walker (Orthoptera: Gryllidae). *Teleogryllus commodus* is a common species of field cricket found in rural and urban environments, including those impacted by artificial light at night (Hill, 1974; G. R. Hopkins, personal observation), throughout southeastern Australia (Otte & Alexander, 1983; Robinson, 2005), and precopulatory mating behaviour of this species is well described (Evans, 1983; Loher, 1979; Loher & Orsak, 1985). Approximately 2 h prior to sunset, adult males commence

production of a stereotypic advertisement call from inside their underground resident burrow (Hill, Loftus-Hills, & Gartside, 1972). Adult females use these calls to locate adult males (Evans, 1983; Loher, 1972), but other males may also respond to the resident male advertisement calls with an aggressive or territorial call (Evans, 1983). Thus, while males typically call from a dark burrow, potential mates or rival males may need to traverse a lit environment to locate the caller. Our experiment thus assessed simultaneously whether the presence of a male advertisement call (broadcast through a speaker at the far end of an arena) affected male and female movement patterns in the presence and absence of a light barrier in an otherwise dark arena. Given the importance of male acoustic communication and because this species has been observed inhabiting artificially lit urban environments, we hypothesized that male calling behaviour would have a greater influence on movement patterns than the presence of night lighting in this species.

METHODS

Experimental Animals

Experimental crickets ($N = 66$ virgin females, 41 virgin males) originated from a stock population that were collected from Kinglake, Victoria, Australia (37°27′50″S, 145°11′53″E) in 2010 and had been maintained in the laboratory for 15 generations under standard rearing conditions (12:12 h light:dark cycle (500:0 lx, no ALAN); 26 °C; Durrant et al., 2015). Following their final moult, crickets were transferred to individual clear plastic containers (15 × 9 cm and 5 cm height) for 2 weeks to ensure sexual maturity (Durrant, Botha, Green, & Jones, 2018). Each cricket was provided with six pellets of dry cat food (Friskies, Senior Splendor, Rhodes, New South Wales, Australia) every 2–3 days, ad libitum water and a single piece of a standard cardboard egg carton for shelter.

Ethical Note

As *T. commodus* is a common endemic insect and is not protected under Australian conservation laws, no permits or ethics approval were needed to maintain or utilize this species in
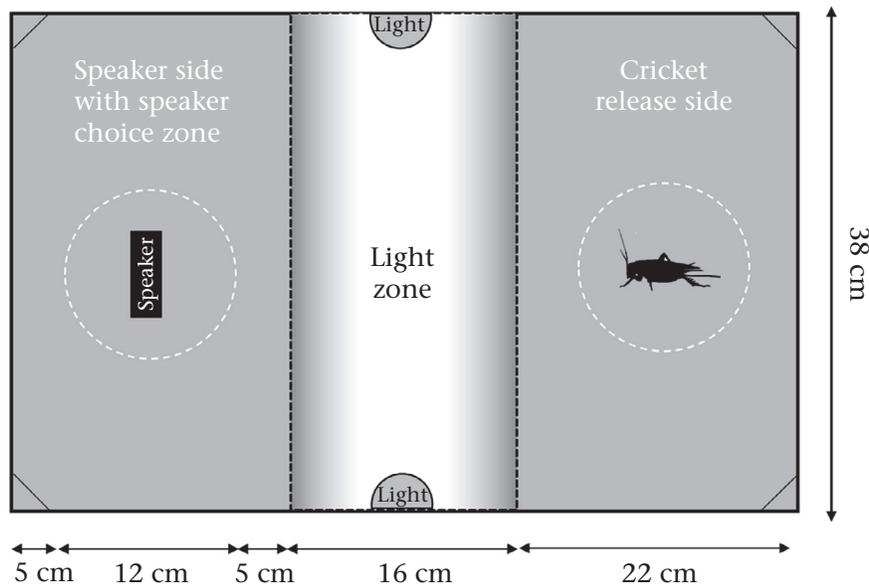

Figure 1. Experimental arena used in phonotaxis trials, showing the location of the release site of the cricket (centre of the 'cricket release side'), the speaker (black rectangle in the 'speaker choice zone') and two LED lights (grey half-moon shapes) located 27 cm above the central 'light zone'. Cricket and speaker images are not to scale.

research. Crickets were housed individually to reduce aggressive encounters, and handling was kept to a minimum. At the conclusion of experiments, experimental crickets were maintained for the remainder of their lives under standard laboratory conditions (see above).

Experimental Arena

Crickets were tested in an open-top corrugated cardboard experimental arena (60 × 38 cm and 36 cm height; Fig. 1) located in a dark climate-controlled laboratory (mean 26 °C to match housing conditions, range 25–28 °C, measured by a digital thermometer placed beside the experimental arena at the start of the trial). The arena had bare walls and was insulated from ground vibrations by 5 cm thick acoustic foam. We placed tape on the floor and sides of the arena to prevent the crickets from escaping up the sides of the box and Play Sand (Richgro Garden Products, Jandakot, Western Australia, Australia) on the floor to facilitate cricket movement along the ground (modified from Judge, Ting, & Gwynne, 2014). Preliminary trials demonstrated that crickets preferentially remained in the corners of any holding container; thus, to ensure movement, we curved the corners of the experimental arena using tape and cardboard buffers. At one end of the arena, we placed a self-powered loud speaker (7 × 3 cm and 8 cm tall; see Playback System below for details) on the floor 5 cm from one of the narrow walls of the experimental arena (Fig. 1). The speaker was directed at the opposite wall and thus in practice faced the cricket when it was placed in the arena. To control for potential end preference, we alternated the end of the arena at which we placed the speaker for each trial.

Experimental Treatments

Prior to the start of the experiment, crickets were assigned to one of four treatment groups that varied in the presence or absence of a light barrier (Lights-on versus Lights-off), and whether a male advertisement call was broadcast or not from a speaker (Call-on versus Call-off; see Table 1 for all sample sizes). Each subject was used only once and only in one experiment/trial.

Creating a light barrier

To create a central light barrier, we suspended two round (4 cm diameter) light-emitting diode (LED) Push Lights (MagicLiving, 6700 K, $\lambda_p = 450$ nm; Melbourne, Australia) 27 cm above the centre of the experimental arena, ensuring that the light emitted was directed downwards onto the arena floor (Fig. 1). For Lights-on trials, this resulted in a 5 cm central strip of light running across the width of the experimental arena (mean ± SD intensity of light = 14.57 ± 2.32 lx; measured using a SKL300 light meter, Skye Instruments Ltd, Wells, U.K., 2 cm (height of probe) above the floor of the experimental arena). The central strip was surrounded on either side by a 5.5 cm strip of dimmer lighting (mean ± SD intensity of light = 1.37 ± 0.68 lx) and left both ends of the arena in relative darkness (mean ± SD intensity of light = 0.20 ± 0.30 lx). These levels of illumination were chosen to be representative of those found under and around urban streetlights, both generally (Gaston et al., 2014) and specifically where crickets are naturally found in Melbourne, Australia (mean ± SE = 9.0 ± 0.34 lx; range

4.1–16.69 lx; $N = 30$ lights; G. R. Hopkins & M. T. Lockett, personal measurements).

Creating an average male advertisement call

Male *T. commodus* produce a stereotypic attraction call composed of a single chirp followed by a variable number of trills (Hill et al., 1972; Loher & Rence, 1978). We constructed an 'average' male *T. commodus* advertisement call using Audacity v.2.1.1 (http://audacity.sourceforge.net) from recordings of six males from the laboratory stock population (recorded under standard conditions in the stock population laboratory at 26 °C). We manipulated an existing recording of a male to match the mean values for call duration (2.06 s), chirp length (0.311 s), trill length (0.652 s), pulse number (19.5) and dominant frequency (4.01 kHz), calculated from those six males (see Drayton, Milner, Hunt, & Jennions, 2010; Hill et al., 1972; Loher & Rence, 1978 for details and definitions of advertisement call parameters).

Playback system. During Call-on trials, the advertisement call was broadcast from a self-powered JBL GO portable loudspeaker (7 × 3 cm and 8 cm tall; Harman International Industries, Northbridge, CA, U.S.A.) connected remotely via Bluetooth to a mobile phone (iPhone 5S). The call was broadcast on a 10 min loop with 2.3 s of silence between each call. The sound pressure level (SPL) of broadcast calls measured above the speaker was set to a mean (± SD) of 60.23 ± 1.25 dB (approximating the volume of a male *T. commodus* calling in the field; Hill et al., 1972) using a Digitech Q-M-1589 sound level meter with 'A' frequency weighting ('A' frequency weighting is appropriate given the dominant frequency of 4.0 kHz for this species' advertisement call). The sound level meter was held directly parallel with the floor, and in line with the top of the experimental arena. The SPL of the playback was measured at the start of each trial. The speaker was present for all trials, regardless of whether a call was broadcast.

Experimental Procedure

Experiments took place between 1800 and 2000 h Eastern Australian Summer Time between October and December 2017. This was approximately 2 h prior to laboratory sunset, coinciding with the daily onset of male calling behaviour in this species (Loher, 1972; G. R. Hopkins, personal observation). To enable detection of crickets, we placed a 25 W 240–250 V Mirabella incandescent red light (following Hunt, Brooks, & Jennions, 2005) 185 cm above the arena floor. For the last 20 crickets tested, this bulb failed and was replaced with a white bulb surrounded with thick red plastic to replicate the same conditions. There was no significant difference in the mean lux present throughout the experimental arena with the two bulbs (t tests: all $P > 0.05$). Regardless, we blocked all subsequent analyses by bulb type to account for any subtle variation in lighting conditions (see below). This red light cast minimal illumination on the arena (1.1 lx at its brightest), and was most likely not perceived by the crickets, as crickets (family Gryllidae) have peak spectral sensitivities (wavelengths of maximum absorbance) at ~335, 440 and 517 nm (Zuffal, Schmitt, & Menzel, 1989 cited in ; Davies, Bennie, Inger, De Ibarra, & Gaston, 2013), which is well outside of the spectral range of red light (635–700 nm; Davies et al., 2013). To assess whether our four treatment groups influenced cricket

Table 1
Samples sizes (analysed) for males and females across the four light and call treatments

	Lights-on/Call-on	Lights-on/Call-off	Lights-off/Call-on	Lights-off/Call-off
Female	16	18	15	17
Male	12	10	10	9

movement, we subdivided the experimental arena into three zones (release zone, central zone, speaker zone; Fig. 1). Within the speaker zone, we further defined a circular speaker choice zone (12 cm diameter) that surrounded the speaker (Fig. 1).

Behavioural trials lasted a total of 10 min per individual. At the start of a trial, we introduced a restrained cricket (under a circular, 12 cm diameter, plastic container) to the release zone (10 cm from the short edge of the arena). For Lights-on trials, we turned on and measured the two LED lights prior to introduction of the cricket to the release zone. After a 2 min acclimation period, we released the cricket from the container. For Call-on trials, we simultaneously commenced broadcasting the male advertisement call. Crickets were tested once only. To reduce the likelihood that chemical cues interfered with subsequent trials, we thoroughly raked the sand and used 70% ethanol to wipe the sides of the arena and all handling containers after each trial (following Judge et al., 2014).

Before and after each trial, we weighed crickets to the nearest 0.001 g on a digital scale. Once all trials were complete, we measured the left hindfemur (mm) as a proxy for body length using digital callipers (Durrant et al., 2018). We determined body condition from the residuals of the regression of body weight (pretrial) and femur length (Botha et al., 2017).

Video Analysis

Trials were videorecorded using a Canon LEGERIA HF R406 digital video camera and behaviours subsequently scored using the behavioural software program BORIS v.4.1.10 (Friard & Gamba, 2016). From the videos, we scored the time to move initially (s), time spent in the central zone (s), time to reach the speaker zone (taken as when the head entered the zone) after the initial movement (s), time spent in the speaker zone (s), number of times the speaker was touched by the cricket's antennae, total time spent active or exploring the arena (s; defined as total time − (time spent immobile + time trying to escape the arena)), and finally, for male trials, whether or not the male produced an aggressive or territorial call (easily distinguished from attraction calls by the presence of a single loud chirp with no trills; Loher & Rence, 1978). Videos were analysed in a random order by two observers (N.L.C., E.K.T.).

Statistical Analysis

Data from 12 crickets were not included in statistical analyses: six crickets spent less than 1 min moving during the entire 10 min period (Lights-on/Call-on = 3 females; Lights-off/Call-off = 1 female; Lights-off/Call-on = 1 male; Lights-on/Call-on = 1 male); two males (Lights-on/Call-on treatment) escaped by climbing the sides of the experimental arena; two females (Lights-on/Call-off = 1, Lights-off/Call-on = 1) and one male (Lights-on/Call-on) were discarded due to experimental error and a final female (Lights-off/Call-off) died the day after the experiment. Final analysed sample sizes for each treatment are included in Table 1.

For the remaining crickets, variation in the observed behaviours was explored in R (R Core Team, 2016) using mixed-effects models with the packages 'lme4' (Bates, Maechler, Bolker, & Walkder, 2015) and 'lmerTest' (Kuznetsova, Brockhoff, & Christensen, 2016). Light treatment, call treatment, sex and the interaction between these factors were included as categorical main effects; leg length, body condition and ambient temperature were included as continuous main effects. Whether the speaker zone was on the left or right end of the arena, the date of the experiment and the red bulb type (see above) were included as random effects in all models. Maximal models were simplified by removing interactions and terms with a significance of $P > 0.10$ (apart from light and call treatments, and sex, which were retained because they were of primary interest to our

hypotheses). Significance of terms in final models were assessed with $\alpha = 0.05$. Differences in levels of significant factors were examined post hoc using Tukey-adjusted multiple comparisons with the package 'lsmeans' (Lenth, 2016).

RESULTS

Initial Movement

Crickets took significantly longer to initially move in the Lights-on treatment compared to the Lights-off treatment ($P = 0.02$; Table 2, model a). In contrast, the time to first movement was comparable for females and males ($P = 0.77$, Table 2, model a) and was unrelated to whether a call was broadcast from the speaker ($P = 0.84$, Table 2, model a).

Time Spent in the Central Zone

The average time spent in the central (lit) zone was unrelated to light treatment, call treatment, or sex of the cricket (Table 2, model b).

Likelihood of Reaching the Speaker Zone

Overall, crickets were more likely to reach the speaker choice zone during the Call-on treatment than the Call-off treatment ($P = 0.002$; Table 2, model c); however, this relationship was driven by an interaction between call treatment and sex (Table 2, model c). Post hoc Tukey's tests revealed that females were more likely to reach the speaker choice zone in the Call-on treatment than the Call-off treatment ($P = 0.001$; Fig. 2). In contrast, males were equally likely to reach the speaker regardless of whether a call was broadcast or not ($P > 0.05$; Fig. 2). There was a negative relationship between cricket body condition and the likelihood that the cricket entered the speaker choice zone ($\beta = -9.09 \pm 3.28$, $P = 0.006$; Table 2, model c) and crickets were marginally more likely to enter the speaker choice zone during the Lights-on treatment (mean $\pm$ SE proportion = 0.80 ± 0.06) compared to the Lights-off treatment (mean $\pm$ SE proportion entering the speaker choice zone = 0.64 ± 0.07; $P = 0.07$; Table 2, model c).

Time to Reach the Speaker Choice Zone

The time taken to reach the speaker choice zone was unrelated to light treatment or sex (both $P > 0.80$; Table 2, model d). However, crickets reached the speaker choice zone significantly faster in the Call-on treatment compared to the Call-off treatment ($P = 0.003$; Table 2, model d).

Time Spent in the Speaker Choice Zone

Crickets spent longer in the speaker choice zone when a call was broadcast compared to when the speaker remained silent ($P = 0.003$; Table 2, model e). Females spent consistently longer in the speaker choice zone than did males ($P < 0.001$; Table 2, model e), but there was a significant interaction between light treatment and sex ($P = 0.003$; Table 2, model e). Post hoc comparisons revealed that the time spent by females was comparable for the Lights-on and Lights-off treatments ($P > 0.05$; Fig. 3). In contrast, males spent marginally longer in the speaker choice zone during the Lights-on treatment compared to the Lights-off treatment ($P < 0.05$; Fig. 3). There was a negative relationship between time spent in the speaker choice zone and body size (effect of femur length: $\beta = -0.73 \pm 0.19$, $P = 0.0003$; Table 2, model e).

Table 2
Results from linear mixed models examining the effects of light treatment, calling treatment, sex, and their interactions; and other covariates (body size, condition, temperature) on all measured behaviours

Model	Median (IQR) for models ab, d—f	Proportion for model c	Statistic	P
(a) Time to first move (s) (log transformed)				
Light treatment (lights-on vs lights-off)	10.8 (3.46—125.8)	6.04 (0.83—136.6)	$F_{1,84.2} = 5.53$	**0.02**
Call treatment (call-on vs call-off)	8.75 (0.95—123)	8.71 (0.99—184.1)	$F_{1,81.3} = 0.04$	0.84
Sex (female vs male)	8.75 (0.95—123)	7.72 (1.45—141.2)	$F_{1,34.3} = 0.09$	0.77
(b) Time spent in the central zone (s)				
Light treatment (lights-on vs lights-off)	116.6 (91.23—180.58)	128.1 (85.27—183.34)	$F_{1,80.6} = 1.89$	0.17
Call treatment (call-on vs call-off)	120.4 (93.11—158.36)	136.39 (77.67—201.80)	$F_{1,75.7} = 2.07$	0.15
Sex (female vs male)	120.2 (79.93—177.23)	142.8 (101.43—199.40)	$F_{1,26.9} = 2.05$	0.16
(c) Likelihood of reaching the speaker zone				
Light treatment (lights-on vs lights-off)	37/46	32/50	$\chi^2_1 = 3.25$	0.07
Call treatment (call-on vs call off)	42/49	27/47	$\chi^2_1 = 9.69$	**0.002**
Sex (female vs male)	44/59	25/37	$\chi^2_1 = 0.08$	0.78
Call treatment × sex			$\chi^2_1 = 6.11$	**0.013**
Body condition			$\chi^2_1 = 7.68$	**0.006**
(d) Time to reach the speaker choice zone after initial move (s)				
Light treatment (lights-on vs lights-off)	175.0 (31.6—421.4)	188.5 (41.6—362.8)	$F_{1,56.8} = 0.03$	0.86
Call treatment (call-on vs call-off)	132.5 (17—334)	256.0 (28—421.4)	$F_{1,62.1} = 0.04$	**0.003**
Sex (female vs male)	175.5 (17—418)	195 (28—415.8)	$F_{1,24.7} = 0.01$	0.92
(e) Time spent in speaker choice zone (s) (log transformed)				
Light treatment (lights-on vs lights-off)	3.36 (1.66—5.04)	3.08 (0.65—5.33)	$F_{1,62} = 0.17$	0.68
Call treatment (call-on vs call-off)	3.87 (0.96—5.25)	2.72 (1.31—3.89)	$F_{1,62} = 8.16$	**0.006**
Sex (female vs male)	3.83 (2.02—5.25)	2.59 (0.27—4.15)	$F_{1,62} = 22.30$	**<0.0001**
Light treatment × sex			$F_{1,62} = 9.78$	**0.003**
Leg length (mm)			$F_{1,62} = 15.10$	**0.0003**
(f) Number of times touching speaker (log+1 transformed)				
Light treatment (lights-on vs lights-off)	0.69 (0—2.71)	0 (0—2.48)	$F_{1,80.9} = 0.60$	0.44
Call treatment (call-on vs call-off)	1.39 (0—2.94)	0 (0—1.10)	$F_{1,75.6} = 40.81$	**<0.0001**
Sex (female vs male)	1.10 (0—2.78)	0 (0—1.10)	$F_{1,31.3} = 17.91$	**<0.0001**
Call treatment × sex			$F_{1,76.2} = 23.48$	**<0.0001**
Leg length (mm)			$F_{1,87.0} = 6.45$	**0.01**
(g) Time spent exploring (s)				
Light treatment (lights-on vs lights-off)	477.0 (186.2—583.2)	471.3 (208.7—580.7)	$F_{1,90} = 0.23$	0.63
Call treatment (call-on vs call-off)	484.2 (295.1—587.8)	461.7 (124.5—561.9)	$F_{1,90} = 2.71$	0.10
Sex (female vs male)	487.9 (229.0—584.0)	467.6 (178.7—562.9)	$F_{1,90} = 0.56$	0.45
Call treatment × sex			$F_{1,90} = 4.61$	**0.01**
Temperature (°C)			$F_{1,90} = 6.78$	**0.03**

Results show simplified models, with nonsignificant ($P > 0.10$) covariates and interactions removed. Bold P values indicate statistical significance ($P < 0.05$). Median and interquartile ranges and/or proportions for each treatment level are also given; interactions are displayed in Figs 2—5, and β values for continuous factors are reported in the text.

Number of Times the Speaker Was Contacted

The number of times a cricket touched the speaker was unrelated to the light treatment ($P = 0.44$; Table 2, model f), but varied

between the sexes across the two call treatments (interaction between call treatment and sex: $P < 0.0001$; Table 2, model f). Post hoc comparisons revealed that females contacted the speaker significantly more often in the Call-on treatment compared to Call-
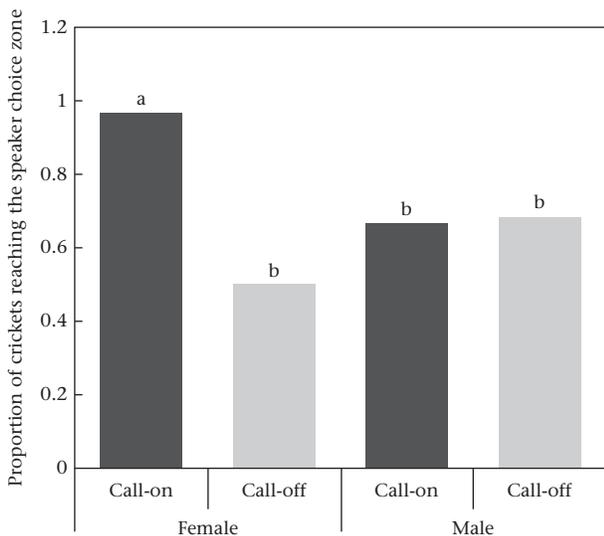

Figure 2. The proportion of female and male crickets reaching the speaker choice zone in the Call-on and Call-off treatments. Different letters denote Tukey-adjusted significant differences across treatments.
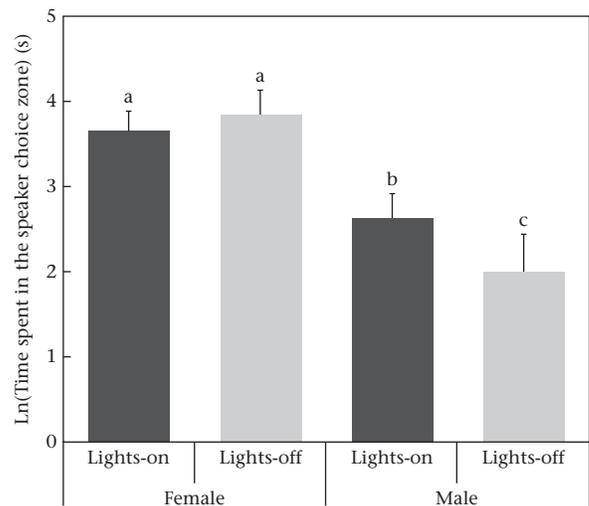

Figure 3. The average time spent by female and male crickets in the speaker choice zone (ln-transformed data) in the Lights-on and Lights-off treatments. Errors bars represent standard errors about the mean. Different letters denote Tukey-adjusted significant differences across treatments.
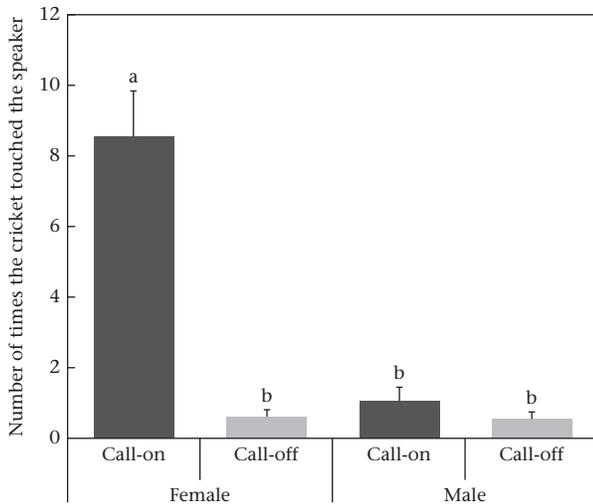
Figure 4. The number of times female and male crickets touched the speaker in the Call-on and Call-off treatments. Errors bars represent standard errors about the mean. Different letters denote Tukey-adjusted significant differences across treatments.

off treatment ($P < 0.0001$; Fig. 4). In contrast, males were equally likely to touch the speaker regardless of whether the call was broadcast or not ($P = 0.28$; Fig. 4). There was a negative relationship between cricket size (femur length) and the number of times an individual touched the speaker ($\beta = -0.22 \pm 0.10$; $P = 0.0003$; Table 2, model f).

Time Spent Actively Exploring

The total time spent exploring during a trial was unrelated to the main effect of light treatment, call treatment or sex (all $P > 0.10$; Table 2, model g). However, females (but not males) spent more time exploring in the Call-On treatment compared to the Call-off treatment (interaction between call treatment and sex: $P = 0.01$; Table 2, model g, Fig. 5). Finally, the time spent exploring was negatively related to temperature ($\beta = -29.37 \pm 12.91$, $P = 0.03$; Table 2, model g).
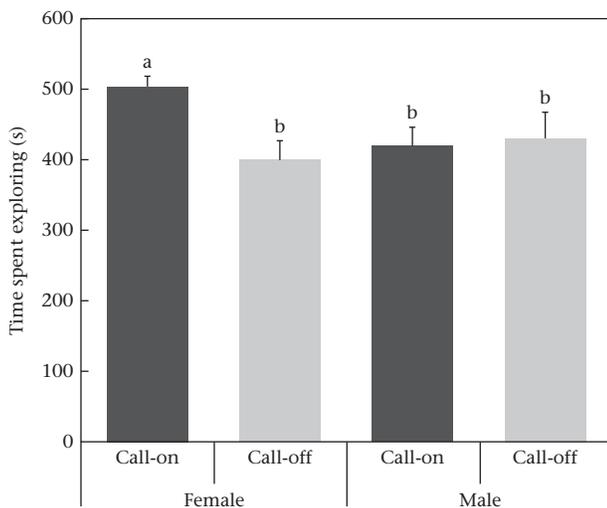

Figure 5. The time spent exploring (s) by female and male crickets in the Call-on and Call-off treatments. Errors bars represent standard errors about the mean. Different letters denote Tukey-adjusted significant differences across treatments.

Male Calling

No males produced aggressive (or advertisement) calls in any of the trials, regardless of lighting or call treatments.

DISCUSSION

Shifts in behaviour are often the first and most visible response of animals to human-induced environmental change, such as the presence of artificial light at night (ALAN) (Wong & Candolin, 2015). However, the degree to which ALAN modifies behaviour may depend on the current trade-off that an animal faces. Here, we experimentally investigated the effect of a light-fragmented environment on the behaviour of adult male and female crickets in the presence and absence of a male attraction call. Our data suggest that, for sexually mature crickets, the effect of ALAN on behaviour was diminished relative to the presence of a broadcast male call, thus supporting our main hypothesis. Predictably, given its role in female mate choice, the effect of the male advertisement call was typically stronger for females than for males, but both sexes modified aspects of their behaviour in its presence regardless of whether their immediate environment was fragmented by artificial light at night or not.

While the presence of ALAN, and thus a fragmented nocturnal environment, did not ultimately inhibit crickets from exploring the arena and reaching the speaker choice zone, it did affect some aspects of mate-finding and exploratory behaviour. Specifically, in support of our hypothesis, the time to commence initial movement at the start of a trial was longer for both sexes when the central zone was illuminated (i.e. during the Lights-on treatment) even in the presence of a male call. It is possible that this may be an adaptive predator-avoidance strategy (Tierney et al., 2017), as many visual predators hunt under artificially lit conditions (Heiling, 1999; Perry et al., 2008). Whether this time difference (~4 s) between treatments is biologically significant and whether such an effect would remain under lower light levels need to be explicitly investigated. Previous work has shown that the presence of ALAN can disrupt some aspects of mating behaviour (Botha et al., 2017), suggesting that ALAN may drive subtle shifts in reproductive parameters and thus may impose some fitness costs. Nevertheless, our data suggest that the light corridor we created did not act as an ecological trap (sensu Hale & Swearer, 2016) − crickets did not spend longer in the central zone when the lights were turned on, nor did the light corridor act as a barrier to movement, as has been observed for other animals (Mathews et al., 2015; Stone et al., 2009). Crickets also did not avoid crossing the light corridor to reach the speaker choice zone. Whether crickets would be as willing to cross a larger, more brightly lit barrier than used here remains to be tested. We note, however, that our data are in line with natural light-related patterns of cricket behaviour. Typically, male calling commences approximately 2 h prior to sunset (Loher, 1972; G. R. Hopkins, personal observation) when light levels are declining but are still significantly higher than the levels used in this experiment. Moreover, our observations in city parks suggest that female crickets will cross artificially lit areas (brighter than the light corridor used in the present study) to reach calling males even after sunset (Fig. 6). How often this occurs in the wild has, however, not been quantified. Finally, it should be noted that this lack of avoidance of artificially lit habitats is not necessarily adaptive, as many insectivorous predators congregate around lights at night (Heiling, 1999; Perry et al., 2008). The specific predation risks for field crickets not avoiding artificial light at night in the wild, and whether these risks are offset by potential mating opportunities, have yet to be explored.

Figure 6. Observations of an acoustically orienting female *T. commodus* in a city park in suburban Melbourne, Victoria, Australia, in February 2018, crossing a lit area. The female cricket (indicated with red arrow) was traversing across a pedestrian path lit by a streetlight (metal pole in centre of image in (a)) towards males calling in dark patches of ground on the other side of the path. (b) Detailed image of the female cricket. Photos taken without flash illumination.

Given the importance of the male attraction call for mating success, and female mate choice in particular, it is not surprising that females responded more strongly to this cue than did males. For males, the increased latency in initial movement may result in a decrease in aggressive behaviours associated with acoustic signalling for territory and suitable sites for burrows, as latency to become active in a novel environment is negatively associated with intraspecific aggression in crickets (Kortet & Hedrick, 2007). We found that males did not respond to the broadcast call of a conspecific by producing their own aggressive call. This finding is in contrast to observations of *T. commodus* in the wild, where males often call aggressively in response to a rival male's advertisement call (Evans, 1983). This absence of aggression may be due to our laboratory setup, as neither another male nor a female was physically present in the arena. It is also conceivable that aggressive interactions are reduced in our generation-15 laboratory-reared crickets. We note this result aligns with studies in other species of crickets (e.g. *Teleogryllus africanus*, and numerous species of *Gryllus*), which found that male aggressive calling in response to other males' calls is inconsistent in a laboratory environment (Cade & Wyatt, 1984). Nevertheless, we found that all tested individuals of *T. commodus*, regardless of sex, did reach the speaker zone faster and spent more time around the speaker when an advertisement call was being played, suggesting that males are responding to the call's presence, but perhaps do not see it as a threat to their reproductive success (Evans, 1983).

Our results also confirm the importance of body size and condition affecting reproductive behaviours in field crickets (Judge et al., 2014). Specifically, crickets with lower body condition were more likely to reach the speaker choice zone than crickets with higher body condition, but within this subset of crickets, smaller crickets contacted the speaker less frequently than larger crickets and spent longer in the speaker choice zone. These differences may arise due to the advertisement call used – the call we created was an average, rather than the highest-quality, male advertisement call. If females in better condition are higher-quality individuals, then they may be more choosy and thus take longer to choose a perceived average quality mate than females in lower body condition (Judge et al., 2014). However, the effects of body condition were comparable for males and females, suggesting that perhaps high-quality males are less likely to engage a rival male (Shackleton, Jennions, & Hunt, 2005). An alternative explanation is that variation in body condition may have influenced movement patterns (Kortet & Hedrick, 2007; Väänänen, Kortet, & Rantala, 2006). If this holds, then this may be further exacerbated because chronic exposure to ALAN affects body condition (Durrant et al., 2018) and immune function (Durrant et al., 2015) in this species.

In conclusion, our data confirm what we predicted given the natural history of *T. commodus*, namely that while both sexes respond to the presence of a male attraction call, the presence of a light-fragmented environment neither acts as an ecological trap nor completely inhibits mating behaviour. Whether the presence of comparable light-fragmented environments disrupts movement patterns and mate-finding behaviour in more strictly nocturnal species, especially those that use celestial cues to find mates and food (e.g. Nørgaard, 2005; Warrant, Dacke, 2016) requires further investigation.

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