



Roaming Romeos: male crickets evolving in silence show increased locomotor behaviours



Susan L. Balenger*, Marlene Zuk

Department of Ecology, Evolution and Behavior, University of Minnesota, Twin Cities, MN, U.S.A.

ARTICLE INFO

Article history:

Received 23 July 2014

Initial acceptance 29 August 2014

Final acceptance 25 November 2014

Available online 28 January 2015

MS. number: A14-00587R

Keywords:

behavioural plasticity

flatwing

sexual selection

signal loss

Teleogryllus oceanicus

Loss of sexual signals should be strongly selected against when these signals are necessary for mate attraction or acquisition. Male *Teleogryllus oceanicus* field crickets produce a long-distance calling song to attract females. Separate genetic mutations recently evolved on the Hawaiian Islands of Kauai and Oahu, rendering approximately 90% and 50% of males, respectively, incapable of calling. We examined whether males from three populations, each with a distinct prevalence of this silent 'flatwing' phenotype, show behavioural plasticity in response to being reared in a call-less environment. Crickets from Kauai, Oahu and Mangaia, a Cook Islands population without the flatwing phenotype, either were or were not exposed to calling song during late juvenile and early adult development. Movement assays showed that when males originating from Kauai were reared in silence, they moved sooner, moved more and spent more time walking during silent behaviour trials than did their counterparts reared with calling song. Males from Oahu and Mangaia, however, showed no such effect of acoustic rearing environment on these behaviours. This suggests that there has been directional selection on Kauai for males to respond to a silent environment by increasing their mobility, thus compensating for their lack of song and increasing their chance of encountering receptive females.

© 2015 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Sexual signals can be crucially important for both the ability to locate potential mates and mating itself. Nevertheless, sexual signals have been lost over evolutionary time in a variety of taxa (Wiens, 2001). Such losses may occur because the signal (typically produced by the male) is no longer useful to its receiver (typically the female) or because natural selection against production of the signal has shifted to outweigh the reproductive benefits gained by its production. For example, populations of threespine sticklebacks, *Gasterosteus aculeatus*, vary widely in expression of male red nuptial coloration, and it is thought that this is due to a loss of redness by populations inhabiting darker environments where colour-based signalling is masked (McDonald, Reimchen, & Hawryshyn, 1995; Reimchen, 1989). Females from these populations still prefer red males when placed in less turbid environments (McKinnon, 1995). *Poecilia reticulata* guppies, on the other hand, provide a classic example of a shift driven by the costs of producing the signal (increased predation) outweighing the reproductive benefits gained (Ender,

1978). Presence of particular predators in streams inhabited by these guppies cause a rapid shift in conspicuousness of coloration and pattern exhibited by males, such that males are under strong selection for crypsis in the presence of predators (Ender, 1980).

Little is currently known about the loss of sexual signals over a contemporary timescale (100 generations or fewer), and only a few well-documented examples exist (Svensson & Gosden, 2007; Zuk & Tinghitella, 2008). This is likely due to the subsequent difficulty that individuals face in obtaining mates when a demonstrably important sexual signal disappears. For example, in many taxa such signals facilitate mating opportunities by helping females find stationary males (Alexander, 1961).

Loss of sexual signals could, therefore, require not only a change in female mate attraction criteria, but also in strategies for mate searching. Behavioural plasticity is a likely mediator of the rapid loss of such traits, since many behaviours are flexible over the life of an organism in ways that accommodate adaptive changes in other traits (Zuk, Bastiaans, Langkilde, & Swanger, 2014). Examples of adaptive divergence of populations resulting from such variation are lacking (Ghalambor, McKay, Carroll, & Reznick, 2007). Population diversification, however, can provide an excellent opportunity to examine the roles of genetic divergence, plasticity, and how

* Correspondence: S. L. Balenger, 1987 Upper Buford Circle, Department of Ecology, Evolution and Behavior, Saint Paul, MN 55108, U.S.A.

E-mail address: sbalenge@umn.edu (S. L. Balenger).

plasticity responds to varying intensities of selection (Ghalambor et al., 2007).

In many North American populations of field crickets, the same male calling song that attracts females also attracts an acoustically orienting parasitoid fly, *Ormia ochracea* (Zuk, Simmons, & Cupp, 1993). Calling is, therefore, subject to both strong natural and sexual selection: calling risks infestation, followed by death, but not calling sharply reduces mating success. In such situations, host acoustic communication is likely to be subject to a trade-off between mate acquisition and death by parasitism. Such trade-offs, however, can be mediated by the existence of noncalling alternative reproductive strategies like satellite behaviours, where males attempt to intercept females that are attracted to the calling of other males, and increased movement, where males increase the likelihood that they will encounter females simply by moving around more.

The Pacific field cricket, *Teleogryllus oceanicus*, has a broad native geographical distribution, including northern Australia and many islands across the South Pacific, including the Cook Islands (Otte & Alexander, 1983). On three of the Hawaiian Islands, *T. oceanicus* and *O. ochracea* have both been introduced, and *T. oceanicus* serves as a host to this parasitoid (Otte, 1994; Zuk et al., 1993). In a remarkable example of rapid morphological evolution of a sexually selected trait, the populations on the Hawaiian Islands of Kauai and Oahu have independently evolved a morphological wing mutation ('flatwing') that renders them obligately silent (Pascoal et al., 2014; Zuk, Rotenberry, & Tinghitella, 2006). Kauai and Oahu populations thus far are consistently found to have approximately 90% and 50% flatwings, respectively. This mutation has likely become established in response to selective pressure from parasitism by *O. ochracea*, even in the face of female sexual selection for male calling song. Other island populations throughout the native range of *T. oceanicus*, like those on the island of Mangaia in the Cook Islands, are not subject to such parasitism and do not exhibit the flatwing phenotype. While natural selection is likely the driving force leading to the emergence and persistence of flatwing males in some *T. oceanicus* populations, it is unclear how the rapid and dramatic loss of an important sexual signal is ultimately maintained over time. Without some sort of compensatory mechanism, the Kauai population would likely have quickly succumbed to extinction.

Previous research has demonstrated that *T. oceanicus* from Kauai reared without exposure to species-typical calling song show both behavioural and morphological plasticity, which is likely to have facilitated their persistence. Kauai females reared without hearing male *T. oceanicus* song show a reduction in choosiness, such that, although they still prefer a male that sings over one that does not, song quality is no longer as important in deciding whether to mate or not (Bailey & Zuk, 2008; Tinghitella & Zuk, 2009). Similarly reared Kauai males, on the other hand, are more likely to approach calling males and engage in satellite behaviour, thus increasing their likelihood of intercepting females should they hear a calling male (Bailey, Gray, & Zuk, 2010).

Increased male phonotaxis in response to an altered acoustic environment suggests that satellite mating tactics could partly be responsible for the persistence of *T. oceanicus* on islands where the flatwing morph is common but calling males still exist. Male phonotactic behaviour is, however, not the only alternative mating tactic used by male crickets (Waltz, 1982). Multiple researchers have noted that some males are seen simply walking around without calling (Cade & Cade, 1992; French & Cade, 1989; Hissman, 1990; Kindvall, Vessby, Berggren, & Hartman, 1998). Such behaviour is akin to that of *Drosophila melanogaster* larvae, which show variation in exploratory behavioural phenotypes in which 'rovers' travel farther while foraging and thus have an advantage over

'sitters' when nutrients are limited (Burns et al., 2012; Graf & Sokolowski, 1989; Sokolowski, 2002). A recent study found that these natural behavioural genetic variants respond to larval nutritional status such that sitters developing in poorer nutritional environments increase their exploratory behaviour as adults (Burns et al., 2012).

Here we ask whether rapid loss of a sexual signal can be accommodated by behavioural plasticity in locomotor behaviours. Specifically, we investigate whether males increase their movement, or exploratory, behaviours in response to the perception of a lack of conspecifics in their local area during late juvenile and early adult development. Such increased movement could in turn increase the likelihood of encountering females, thus enhancing male reproductive success even when they are incapable of producing song and when very few opportunities to act as satellites exist. We propose that males from Kauai, a population of *T. oceanicus* where about 90% of males are flatwing, can increase their likelihood of encountering females and in turn their potential for copulations by increasing the amount of time they spend walking and the distance they travel when they cannot (1) signal their location to females by calling, or (2) satellite around other calling males in the population. To this end we examined the walking behaviour of adult male crickets from Kauai, the population in which calling males are rare, in a call-less environment in response to developing with or without calling song. We predicted that if males reared in call-less environments perceive a lack of calling song as an indication of low population density, then they should invest more time as reproductively mature adults into exploring than males reared in environments full of calling males. We further examined these predictions in two additional populations, each with a different but stable proportion of call-less males (0% in Mangaia, one of the Cook Islands, and ~50% in Oahu). We predicted that, if the traits measured are ubiquitously plastic responses, *T. oceanicus* males should respond to being reared in a call-less environment similarly, regardless of population differences in caller densities. However, if plasticity in locomotor behaviours has provided a selective advantage when callers are rare, the Kauai population should respond to an environment with very few callers by walking more and farther. Males from Mangaia would not be expected to respond to the treatment and so we should find no difference in their locomotor behaviours when reared with and without conspecific song. We made no a priori predictions regarding the response by crickets from Oahu since we do not know whether the reduction in calling song they experience in the wild is sufficient to select for such behaviours.

METHODS

Cricket Populations and Rearing

Distinct colonies of crickets derived from three natural populations were established and maintained in the laboratory. All three populations of crickets originate from island locales: Kauai and Oahu in the Hawaiian Islands, and Mangaia in the Cook Islands. Both Hawaiian Island populations show stable levels of the male flatwing mutation in the wild, but at different levels (~90% on Kauai and ~50% on Oahu). The flatwing mutation does not occur on Mangaia. Details of laboratory population establishment and supplementation are given in Bailey et al. (2010). Briefly, the Kauai colony was established in 2003 upon initial discovery of the flatwing mutation in the wild. The Oahu population was established in 1991. Both Kauai and Oahu are supplemented with the offspring of wild-caught females approximately annually. Mangaia was established in the laboratory in 2009 and has not been

supplemented since. Laboratory colonies consist of a minimum of 100 breeding adults at all times. Cricket colonies are reared in 15-litre containers within temperature- and humidity-controlled incubators (Caron Insect Growth Chambers model 6025) set at 26 °C and 75% humidity with a 12:12 h photoreversed light:dark schedule.

Treatment Groups

Juvenile males were collected prior to their penultimate moult when sex differences become apparent and transferred to individual 118 ml containers containing food (Purina Rabbit Chow), a water vial and egg carton material for shelter. Male crickets housed in individual containers were then randomly assigned to either a 'song' or 'no song' treatment group. The acoustic environment was manipulated by placing 'song' and 'no song' juvenile male crickets in separate incubators. Each treatment incubator was set to the same temperature, humidity and photoperiod conditions as described above. Shelves and walls of the interior of the incubators were lined with sound-absorbing foam. In the 'song' incubator, males experienced population-specific calling song broadcast from Sony SRS-M30 speakers during the 12 h of darkness each day, and no calling song during the 12 h of light. The calling song used was constructed from an average of at least 20 wild male songs recorded from each population (Zuk et al., 2006). This song was played from three CD players at once, each connected to two speakers. Broadcasts were offset between the players so as to give the impression that multiple crickets with the same song parameters were singing. The sound pressure at the container lids was measured inside the incubators with an AZ sound meter (model 8922) and set at 80–85 dB, ensuring that males within the containers experienced calling song at 70–75 dB, the typical intensity of song emanating from a calling male 50 cm away (Bailey et al., 2010; Simmons, Zuk, & Rotenberry, 2001). In the 'no song' incubator, males did not experience calling song during either photoperiod.

Although previous research has found that male wing morph is not associated with the increased phonotaxis and satellite behaviours of males reared without calling song (Bailey et al., 2010), it has been associated with morphological (reproductive tissue mass differs between morphs; Bailey et al., 2010) and physiological (immunity differs between morphs reared without calling song; Bailey, Gray, & Zuk, 2011) responses in similar treatments. Therefore, we determined wing morph for each individual following adult imaginal moult. In the laboratory, the proportion of flatwing males is generally smaller than that found in the field. In our laboratory population from Kauai, approximately 50% of males show the flatwing morphology, while less than 10% and 0% of laboratory males from Oahu and Mangaia, respectively, show the flatwing trait. Therefore, the proportion of flatwings assayed from each population in this study reflects that of the laboratory stocks. The effect of wing morph (flatwing: $N = 54$, normal: $N = 54$) on behavioural traits of Kauai males reared in 'song' and 'no song' environments was not significant for any behaviour (Supplementary Table S1; see Analyses and Results sections below), so data for Kauai individuals were pooled by treatment regardless of wing morph. The number of Oahu juveniles required to obtain an adequate flatwing sample size for a similar analysis was prohibitive; we would have had to isolate approximately 1000 juvenile males to obtain a comparable sample size of Oahu flatwings for each of the two treatments. Ultimately we assayed eight flatwing males and 66 normal-wing males from this population. Results of analyses without flatwing males, however, were qualitatively similar to those with them (Tables S2, S3 give results using only normal-wing males from Oahu), so we present analyses of

treatment effects on Oahu individuals in the results excluding wing morph as a factor. Within 24 h of final adult moult, we surgically removed the scraper from the right wing of all normal-wing crickets to control for sound environment. Although they cannot produce calling song, we also removed a piece of the wing at the same location from flatwing males to control for effects of the surgery.

Movement Trials

All males were tested 8–12 days post-eclosion. Movement trials were conducted in a 23–24 °C anechoic room under red light during 1100–1400 hours. Since crickets were on a photoreversed schedule, these hours corresponded to 2300–0200 hours, during which these crickets are normally active. We performed trials in a 1.5 m² square arena with 0.45 m high walls. A 6 × 6 grid was drawn onto the floor of the arena, for a total of 36 squares measuring 0.25 m² each. The arena floor was covered with accordion-folded metal screening, enabling crickets to move about under cover while still allowing the observer to see all of their movements. In the centre of the arena, a small square was cut out from the screening so that crickets could be placed there to begin trials.

A fresh square of paper was placed in the centre of the arena between each trial to minimize effects of chemical cues between individuals. All males started from the same location. A male was placed on top of the piece of paper and under a fresh 118 ml plastic cup and allowed to acclimate in silence for 5 min. After the acclimation period, the cup covering the male was removed and the silent 10 min trial began.

We recorded when a male began walking after cup removal, defined as the directional movement of at least one body length. We also recorded the amount of time a male spent engaging in directional movement, the number of grid lines crossed and the furthest grid square from the centre reached during the 10 min trial. Grid squares were assigned ranks that corresponded to their relative straight-line distance from the centre of the arena (Supplementary Fig. S1). The number of gridlines crossed provides a proxy measure for the overall distance walked, while the furthest grid square reached provides a measure related to how far from the starting point an individual travelled. These complementary measures are intended to distinguish between a response to treatment in which individuals alter how much walking they are actually doing (i.e. number of gridlines crossed) from one in which individuals simply move farther from the starting point (i.e. furthest grid square reached), which could be seen as an attempt to disperse to an area where they might find conspecifics rather than simply an increase in locomotor behaviour. Time data were collected using the Spectator Go! app for iPads (Bioobserve GmbH, St Augustin, Germany). From this data, we extracted the amount of time a cricket spent walking in the first 2 min after beginning to move and the number of gridlines crossed during this same period. This allowed us to control for latency to begin walking when examining the amount of movement shown by different individuals and populations. Males that failed to move (Kauai: $N = 11$; Oahu: $N = 5$; Mangaia: $N = 28$) were assigned values of 600 s, 0 s, 0 gridlines and 0 grid square as their latency to move, time spent moving, number of gridlines crossed and furthest grid square reached, respectively. We present results from analyses including these 43 males for all behaviours. It is possible, however, that an assignment of 600 s to individuals that did not move during the entirety of the trial could bias the results for this variable since we do not know the true latency value for these individuals. Therefore, we also provide statistics in the text for latency to move when those 43 males were excluded. Finally, we included data for

latency and furthest grid square reached for males that began moving within 480–600 s (Kauai: $N = 9$; Oahu: $N = 4$; Mangaia: $N = 11$), but these individuals were excluded from analyses of time spent walking and number of gridlines crossed because we did not have a full 2 min of data for these behaviours. Ultimately, the following numbers of individuals were assayed from the 'song' and 'no song' treatments, respectively: Kauai: 51, 57; Oahu: 36, 38; Mangaia: 53, 43. Sample sizes for each behaviour, however, vary somewhat due to the aforementioned reasons. Finally, sample sizes for the furthest grid square reached behaviour are smaller for all populations because we did not collect this information for some of the early trials.

Analyses

We first tested whether wing morph of Kauai crickets (normal versus flatwing) affected movement behaviours within 'song' and 'no song' acoustic treatment groups. Latency to move, time spent walking during the 2 min following first movement and number of gridlines crossed during that same 2 min period were all examined for response to wing morph within each treatment group using generalized linear models (GLMs). We used a chi-square analysis to test whether wing morph affected the likelihood that an individual moved at all during the course of the trial. We used multivariate ordinal logistic regression with cumulative logit links to examine

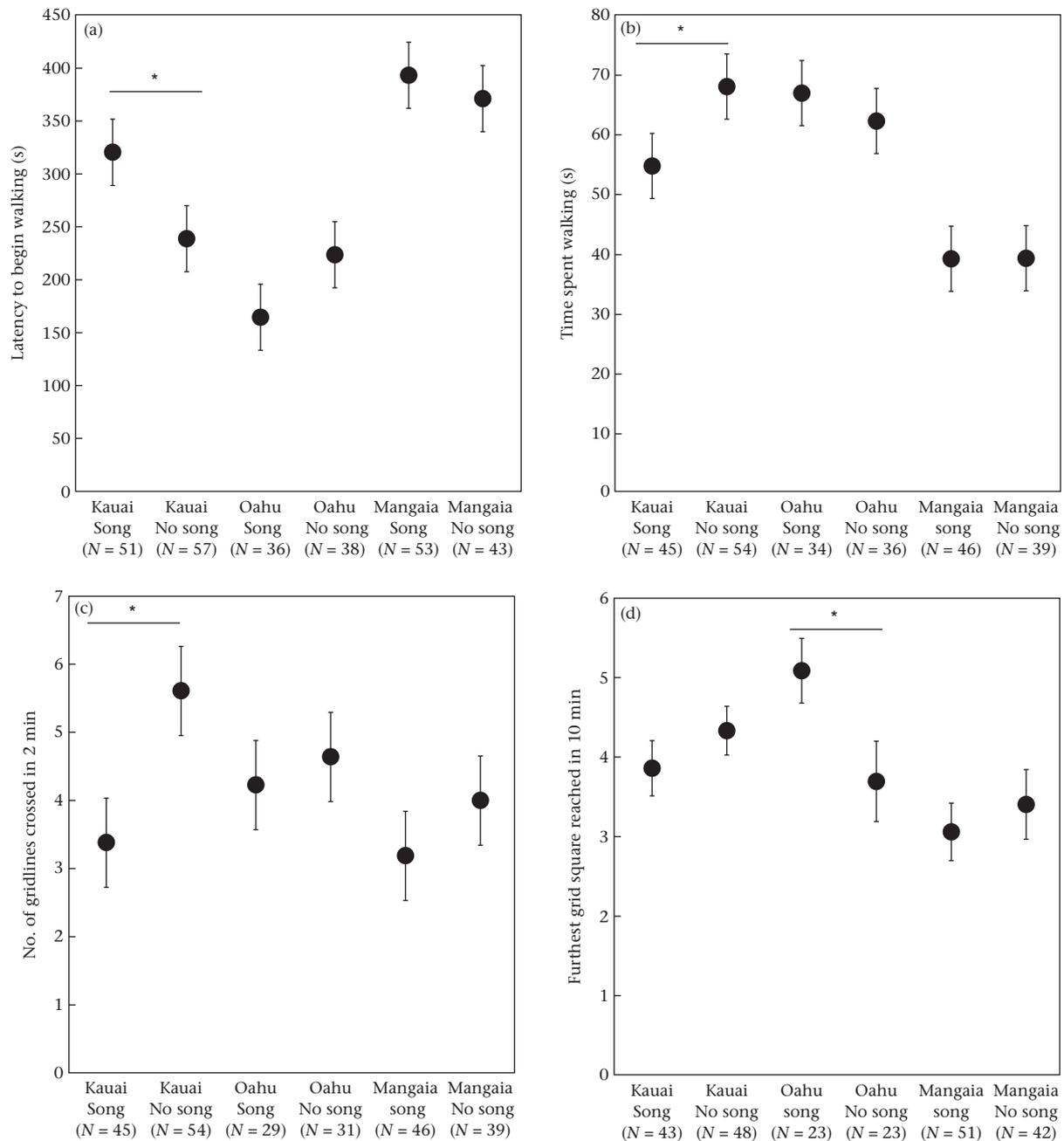


Figure 1. Effect of acoustic rearing environment (with calling song: 'song'; without calling song: 'no song') on (a) latency to begin walking, (b) amount of time spent walking during the 2 min following initial movement, (c) number of gridlines crossed during the 2 min following initial movement and (d) the furthest grid square entered during the 10 min silent trial by adult male field crickets from three populations (Kauai, Oahu, Mangaia) with a distinct prevalence for a silent male morph (>90%, 50% and 0% respectively). Means \pm SE are shown.

the relationship between wing morph and the furthest grid square reached after 10 min.

To test whether crickets from each population respond to a call-less rearing environment by increasing their movement or searching behaviours, we performed similar analyses to those described above that tested for wing morph effects. In this case, however, individuals of both morphs were combined for analyses. Each population was analysed separately because the factor of interest was the effect of acoustic environment on each population. Full GLM models containing population, acoustic environment and their interaction as factors are provided in [Tables S4 and S5](#).

Latency to begin walking, amount of time spent walking and number of gridlines crossed were either square-root or ln transformed to improve normality prior to analyses. All statistical analyses were performed using SAS v. 9.3 (Cary, NC, U.S.A.). Data is available in DataDryad under the identifier <http://dx.doi.org/10.5061/dryad.0hm88>.

RESULTS

Kauai male wing morph (normal wing versus flatwing) had no significant effect on whether a male moved during the trial or not, latency to begin walking, number of gridlines crossed, or the amount of time spent walking (all P s \geq 0.09; [Table S1](#)). We therefore pooled Kauai normal-wing and flatwing male data in all subsequent analyses.

Kauai males reared without calling song began walking sooner, spent more time walking and crossed more gridlines than males from the same population reared in the presence of calling song (excluding individuals that did not move at all, latency to begin walking: $F_{1,95} = 3.44$, $P = 0.07$; [Fig. 1](#), [Table 1](#)). Acoustic environment was not significantly related to the likelihood that a cricket moved at all during the 10 min trial (Fisher's exact test: $P = 0.11$). There was no significant difference in the furthest grid squared reached by the treatment groups ([Table 2](#)).

Oahu males reared without song did not significantly differ in their likelihood to move at all (Fisher's exact test: $P = 1.00$), latency to begin walking, the amount of time they spent walking, or the number of gridlines they crossed when compared to Oahu males reared with calling song (excluding individuals that did not move at all, latency to begin walking: $F_{1,67} = 1.29$, $P = 0.26$; [Fig. 1](#), [Table 3](#)). Males reared with calling song did, however, reach a farther grid square during the 10 min trial ([Fig. 1](#), [Table 2](#)). Males from Mangaia showed no significant difference in their likelihood to move ($\chi^2_1 = 0.43$, $P = 0.51$), nor did they show a significant response to rearing without calling song in any of the other behavioural metrics (excluding individuals that did not move at all, latency to begin walking: $F_{1,66} = 2.18$, $P = 0.14$; [Fig. 1](#), [Tables 2, 3](#)).

DISCUSSION

Male *T. oceanicus* originating from the island of Kauai showed altered movement patterns when reared without hearing conspecific song. These findings demonstrate that flexible behavioural traits may be important in allowing a population to persist when

Table 1
Results of general linear models examining effects of acoustic rearing environment on locomotor behaviours of adult male field crickets from Kauai

	<i>df</i>	<i>F</i>	<i>P</i>	<i>r</i> ²
Latency to begin walking	1, 106	6.58	0.01	0.06
Time spent walking	1, 97	3.97	0.05	0.04
No. of gridlines crossed	1, 97	4.60	0.04	0.05

Significant *P* values are shown in bold.

Table 2

Results of ordinal logistic regressions examining effects of acoustic rearing environment on the furthest grid square reached during the 10 min trial by adult male field crickets from Kauai, Oahu and Mangaia

	χ^2_1	<i>P</i>
Kauai	1.12	0.29
Oahu	6.62	0.01
Mangaia	0.39	0.53

Significant *P* values are shown in bold.

faced with the loss of an important sexual signal. The increase in overall movement matched our predictions for increased walking by males reared in an environment devoid of conspecific calling song if such behaviour facilitates increased mating opportunities. There were no significant differences between Mangaia males reared in the two acoustic environments, while only one metric was significantly different between Oahu males reared with and without calling song. Surprisingly, the direction of that difference was opposite that predicted if males respond adaptively to an environment perceived to be devoid of conspecifics: males reared without calling song travelled less distance during the trial than males reared with calling song.

While previous work has shown a highly heritable component to 'stationary calling' and 'phonotactic satellite' male mating strategies in the field cricket *Gryllus integer*, males are capable of engaging in both behaviours (Cade, 1981). A less commonly discussed behaviour, however, is that of the noncalling, nonsatellite wandering male. Several studies have identified males adopting such a strategy in populations of crickets (*Gryllus campestris*; *Metrioptera roeseli*; Hissman, 1990; Kindvall et al., 1998). On its own, it is thought to be a fairly unsuccessful strategy resulting in few actual copulations (Hissman, 1990; Kindvall et al., 1998). In conditions like those experienced by crickets on Kauai, however, individuals with increased locomotor or exploratory behaviour, combined with increased male phonotaxis and decreased female choosiness, are likely to have greater success at locating potential mates (Bailey et al., 2010; Bailey & Zuk, 2008).

On the other hand, it is also likely that male field crickets that increase their walking activities are subject to energetic costs and increased predation. Hack (1998) found that walking behaviours were more energetically expensive than stridulation by another field cricket, *Acheta domesticus*. Furthermore, cane toads (*Bufo marinus*) and other nocturnal sit-and-wait predators are common on our field sites. Benefits in the form of increased reproductive success gained through increased walking would be weakened if the energetic and survival costs are also increased by this behaviour. The fact that females commonly walk across equivalent distances in response to calling males (Zuk et al., 2006), however, suggests that the costs would not necessarily outweigh the benefits of finding a mate.

Table 3

Results of general linear models examining effects of acoustic rearing environment on locomotor behaviour of adult male field crickets from Oahu and Mangaia

	<i>df</i>	<i>F</i>	<i>P</i>	<i>r</i> ²
Oahu				
Latency to begin walking	1, 72	1.72	0.19	0.03
Time spent walking	1, 68	0.20	0.65	0.00
No. of gridlines crossed	1, 58	0.03	0.85	0.00
Mangaia				
Latency to begin walking	1, 94	0.46	0.50	0.00
Time spent walking	1, 83	0.13	0.72	0.00
No. of gridlines crossed	1, 83	0.88	0.35	0.01

Other researchers have postulated that males should preferentially call at low densities, while at high densities relatively more males should adopt satellite behaviours (Cade & Cade, 1992; French & Cade, 1989; Zuk & Tinghitella, 2008). In the case of the *T. oceanicus* used in this experiment, males had no evidence that calling would attract females: the males were 8–12 days post-adult eclosion and had not encountered any females for over 3 weeks. However, there were also no calling males present during the behaviour trials, precluding them from adopting a satellite tactic. It seems a perfect trajectory to extinction for a population consisting primarily of flatwing males if males strictly adhered to the proposed rule that they should call when density is low. Although flatwing males do not have the wing structures to produce species-typical song, they do still regularly engage in stridulatory behaviours. Flatwing males that sit still and stridulate will, of course, not attract females. Instead, utilizing a mating strategy already in their repertoire (i.e. wandering without calling) is much more likely to be adaptive in this scenario.

Oahu and Mangaia males, on the other hand, do not appear to be using this same strategy in response to life in a call-less environment. In all six groups (three populations and two rearing environments) there was a large amount of variation for all behaviours measured, with every group spanning the entire range of each variable. Thus, it appears that some individuals within each population, regardless of flatwing prevalence in that population in the wild, show increased walking behaviours that could be adaptive in the right circumstances. If the behavioural responses displayed by Kauai males are reproductively advantageous, then one might expect to see selection for similar responses among the Oahu population should the prevalence of callers drop below an undetermined threshold.

That we found population differences in behaviours suggests that there is an underlying genetic component controlling some locomotory and exploratory behaviours of *T. oceanicus*. A recent study found significant additive genetic variance on locomotory performance in *Teleogryllus commodus* jump distance and jump power ($h^2 = 0.3$; Lailvaux, Hall, & Brooks, 2010). Lailvaux et al. (page 1534) argued that these results 'indicate that selection operating directly on male jumping performance has strong potential to result in evolutionary change'. The differences between cricket populations in the current study regardless of treatment (Tables S4, S5) in latency to begin walking, amount of time spent walking and furthest grid square reached suggests that there is also a heritable component to these behaviours that could respond to selection. Counter to arguments for performance-based estimates of fitness, Lailvaux et al. found a negative genetic relationship between measures of mating success, including stridulation effort, and locomotor performance (Lailvaux et al., 2010). While this is a genetic trade-off in *T. commodus*, reduced stridulation effort and increased locomotor investment among *T. oceanicus* males on Kauai would be adaptive because virtually all males there are flatwings. Even though flatwing males are incapable of producing song when they rub their wings together, they do stridulate. It would be interesting to know whether increased locomotion effort among Kauai *T. oceanicus* corresponds to decreased stridulation effort.

Regardless of the underlying genetics, this study provides evidence that behavioural plasticity in response to differences in rearing environment can accommodate the rapid loss of a sexual signal. It appears that field crickets from Kauai are capable of utilizing multiple adaptive behaviours, including increased locomotor behaviour (this study) and satellite behaviour (Bailey et al., 2010) by males and decreased choosiness in females (Bailey & Zuk, 2008), in response to the acoustic environment experienced during late juvenile and early adult stages. The increased likelihood of engaging in alternative reproductive tactics appears to be an important

behavioural response, which can facilitate the continued survival of a population in the face of the incredibly rapid loss of its primary sexual signal. It will be important to consider the role of alternative mating tactics in accommodating sexual signal loss in general as more examples are identified.

Acknowledgments

Thanks to E. Bastiaans and E. Maring for assistance with behavioural assays, J. M. Beatty for building the arena, H. Kunerth, L. Lara, E. Maring, E. Schmidtman and J. Walker for assistance in rearing crickets and two anonymous referees for helpful comments on the manuscript. This work was supported by the University of Minnesota and a National Science Foundation grant to M.Z. (IOS 1261575).

Supplementary Material

Supplementary Material associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2014.12.023>.

References

- Alexander, R. D. (1961). Aggressiveness, territoriality, and sexual behavior in field crickets (Orthoptera: Gryllidae). *Behaviour*, 17, 130–223.
- Bailey, N. W., Gray, B., & Zuk, M. (2010). Acoustic experience shapes alternative mating tactics and reproductive investment in male field crickets. *Current Biology*, 20, 845–849.
- Bailey, N. W., Gray, B., & Zuk, M. (2011). Exposure to sexual signals during rearing increases immune defense in adult field crickets. *Biology Letters*, 7, 217–220.
- Bailey, N. W., & Zuk, M. (2008). Acoustic experience shapes female mate choice in field crickets. *Proceedings of the Royal Society B: Biological Sciences*, 275, 2545–2650.
- Burns, J. G., Svetec, N., Rowe, L., Mery, F., Dolan, M. J., Boyce, W. T., et al. (2012). Gene–environment interplay in *Drosophila melanogaster*: chronic food deprivation in early life affects adult exploratory and fitness traits. *Proceedings of the National Academy of Sciences of the United States of America*, 109, 17239–17244.
- Cade, W. H. (1981). Alternative male strategies: genetic differences in crickets. *Science*, 212, 563–564.
- Cade, W. H., & Cade, E. S. (1992). Male mating success, calling and searching behaviour at high and low densities in the field cricket, *Gryllus integer*. *Animal Behaviour*, 43, 49–56.
- Endler, J. A. (1978). A predator's view of animal color patterns. In M. K. Hecht, W. C. Steere, & B. Wallace (Eds.), *Evolutionary biology* (Vol. 11, pp. 319–364). New York, NY: Springer.
- Endler, J. A. (1980). Natural selection on color patterns in *Peocilia reticulata*. *Evolution*, 34, 76–91.
- French, B. W., & Cade, W. H. (1989). Sexual selection at varying population densities in male field crickets, *Gryllus veletis* and *G. pennsylvanicus*. *Journal of Insect Behavior*, 2, 105–121.
- Ghalambor, C. K., McKay, J. K., Carroll, S. P., & Reznick, D. N. (2007). Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Functional Ecology*, 21, 394–407.
- Graf, S. A., & Sokolowski, M. B. (1989). The rover/sitter *Drosophila* foraging polymorphism as a function of larval development, food patch quality and starvation. *Journal of Insect Behavior*, 2, 301–313.
- Hack, M. A. (1998). The energetics of male mating strategies in field crickets (Orthoptera: Gryllidae). *Journal of Insect Behavior*, 11, 853–867.
- Hissman, K. (1990). Strategies of mate finding in the European field cricket (*Gryllus campestris*) at different population densities: a field study. *Ecological Entomology*, 15, 281–291.
- Kindvall, O., Vessby, K., Berggren, A., & Hartman, G. (1998). Individual mobility prevents an Allee effect in sparse populations of the bush cricket *Metricoptera roeslii*: an experimental study. *Oikos*, 81, 449–457.
- Lailvaux, S. P., Hall, M. D., & Brooks, R. C. (2010). Performance is no proxy for genetic quality: trade-offs between locomotion, attractiveness, and life history in crickets. *Ecology*, 91, 1530–1537.
- McDonald, C. G., Reimchen, T. E., & Hawryshyn, C. W. (1995). Nuptial color loss and signal masking in *Gasterosteus*: an analysis using video imaging. *Behaviour*, 132, 963–977.
- McKinnon, J. S. (1995). Video mate preferences of female three-spined sticklebacks from populations with divergent male coloration. *Animal Behaviour*, 50, 1645–1655.
- Otte, D. (1994). *The crickets of Hawaii*. Philadelphia, PA: Orthopterists' Society.

- Otte, D., & Alexander, R. D. (1983). The Australian crickets (Orthoptera: Gryllidae). In *Proceedings of the Academy of Natural Sciences of Philadelphia, Monograph 22*. Lawrence, KS: Allen Press.
- Pascoal, S., Cezard, T., Eik-Nes, A., Gharbi, K., Majewska, J., Payne, E., et al. (2014). Rapid convergent evolution in wild crickets. *Current Biology*, *24*, 1369–1374.
- Reimchen, T. E. (1989). Loss of nuptial color in threespine sticklebacks (*Gasterosteus aculeatus*). *Evolution*, *43*, 450–460.
- Simmons, L. W., Zuk, M., & Rotenberry, J. T. (2001). Geographic variation in female preference functions and male songs of the field cricket *Teleogryllus oceanicus*. *Evolution*, *55*, 1386–1394.
- Sokolowski, M. B. (2002). *Drosophila*: behavior meets genetics. *Nature Reviews Genetics*, *2*, 879–890.
- Svensson, E. I., & Gosden, T. P. (2007). Contemporary evolution of secondary sexual traits in the wild. *Functional Ecology*, *21*, 422–433.
- Tinghitella, R. M., & Zuk, M. (2009). Asymmetric mating preferences accommodated the rapid evolutionary loss of a sexual signal. *Evolution*, *63*, 2087–2098.
- Waltz, E. C. (1982). Alternative mating tactics and the law of diminishing returns: the satellite threshold model. *Behavioral Ecology and Sociobiology*, *10*, 75–83.
- Wiens, J. J. (2001). Widespread loss of sexually selected traits: how the peacock lost its spots. *Trends in Ecology & Evolution*, *16*, 517–523.
- Zuk, M., Bastiaans, E., Langkilde, T., & Swanger, E. (2014). The role of behaviour in the establishment of novel traits. *Animal Behaviour*, *92*, 333–344. <http://dx.doi.org/10.1016/j.anbehav.2014.02.032>.
- Zuk, M., Rotenberry, J., & Tinghitella, R. M. (2006). Silent night: adaptive disappearance of a sexual signal in a parasitized population of field crickets. *Biology Letters*, *2*, 521–524.
- Zuk, M., Simmons, L. W., & Cupp, L. (1993). Calling characteristics of parasitized and unparasitized populations of the field cricket *Teleogryllus oceanicus*. *Behavioral Ecology and Sociobiology*, *33*, 339–343.
- Zuk, M., & Tinghitella, R. M. (2008). Rapid evolution and sexual signals. In P. d'Ettore, & D. P. Hughes (Eds.), *Sociobiology of communication: An interdisciplinary perspective* (pp. 139–155). New York, NY: Oxford University Press.