Preexisting behavior renders a mutation adaptive: flexibility in male phonotaxis behavior and the loss of singing ability in the field cricket *Teleogryllus oceanicus*

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Flexibility in behavior and other traits can pave the way for rapid evolutionary change. A wing mutation, "flatwing," eliminates the ability of >90% of male field crickets (*Teleogryllus oceanicus*) from one Hawaiian population to produce song to attract females. The morphological change was favored because calling is risky in Hawaii, attracting deadly parasitoid flies. An earlier study suggested that instead of calling, silent flatwing males use satellite behavior, approaching one of the few remaining callers and intercepting females attracted to them. Satellite-like behavior may have existed as a behavioral option prior to the wing mutation, accommodating the loss of singing ability, or behavior may have changed simultaneously with the spread of the mutation. In phonotaxis trials, males from different populations across the crickets' range varied in the distance at which they settled from the source of broadcast song, behaving more or less like satellites. Anecdotally, we noted satellite behavior in all populations, and importantly, males from the mutated population and its direct ancestor behaved similarly. This suggests that the alternative behavior is not strictly associated with the mutation and instead predated the change in morphology. We hypothesized further that satellite behavior may have been preexisting because it is beneficial under other circumstances, such as poor mating success. Virgin males did not show enhanced phonotaxis relative to multiply mated males, however. We conclude that satellite behavior predated the mutation in wing morphology, providing obligately silent males with an alternative method of locating mates and effectively rendering the wing mutation adaptive. Whereas mating history does not appear to influence phonotaxis behavior in males, other factors such as the acoustic environment and demographic conditions may be important contributors to behavioral decisions during male mate location. *Key words:* alternative mating behavior, flatwing, phonotaxis, rapid evolution, satellite. *[Behav Ecol 20:722–728 (2009)]*

Sexual signals are critical for mate location and courtship, but intraspecific variation in mating signals and behavior is pervasive (Darwin 1871; Andersson 1994; Shuster and Wade 2003). For instance, males frequently use alternative mating behaviors such as female mimicry, satellite behavior, or "sneaky mating" to attract mates, and these behaviors are often associated with distinct morphologies (Gross 1996; Shuster and Wade 2003). Alternative mating behaviors can be genetically distinct, such that a given male can only use one (sometimes called strategies), or all males can be genetically monomorphic but utilize one behavior in favor of another under certain conditions, in particular environments, or when their status changes (sometimes called tactics) (Gross 1996). It has been argued, however, that such a dichotomy likely oversimplifies the situation, and many of our examples may actually be from a fairly continuous distribution of mating behaviors (Andersson 1994; Shuster and Wade 2003). Plasticity in behavior and other traits can pave the way for rapid evolutionary change by allowing a trait to be favored that may otherwise be maladaptive (Baldwin 1896; West-Eberhard 2003; Ghalambor et al. 2007).

Field crickets display one commonly investigated example of alternative mating behaviors in which both genetic and environmental components likely play a role. Typically, males are stationary and produce long-distance songs to attract locomotory females from afar (Alexander 1961). Rather than calling, however, some males act as satellites, silently intercepting females who have been attracted to the call of another male (Cade 1975; Hissmann 1990; Zuk et al. 1993). Satellite behavior exists as an alternative for numerous insects and anurans (Gross 1996; Shuster and Wade 2003). Cade (1981a) selected for calling and silent behavior in male *Gryllus integer* and found singing behavior to be about 50% heritable. In *G. integer* (as well as other field crickets), calling males attract phonotactic parasitoid flies, which may in part explain why not all males call (Cade 1979; Zuk et al. 1993). Males may switch from calling behavior to silent satellite behavior even within a night (Rowell and Cade 1993; Hack 1998), and satellite behavior may be preferred because it is less energetically expensive than calling (Hack 1998) or simply because an individual has experienced little success as a caller.

Both female and male field crickets will approach the calling song of conspecifics (Pollack 1982; Kiflawi and Gray 2000). Normally, however, males settle some distance from other signaling individuals. For instance, the Polynesian field cricket, *Teleogryllus oceanicus*, has a nearest neighbor distance of at least 1 m (Zuk M, unpublished data) similar to that found for *G. integer* (Cade 1981b). Male phonotaxis may function in habitat selection, territorial spacing, or the formation of mating

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aggregations (Ulagaraj and Walker 1973; Cade 1979; Campbell and Shipp 1979). When males behave as satellites, however, they show enhanced phonotaxis, coming into extremely close contact with the signaling male, rather than settling some distance away (Cade 1980). Empirical and theoretical work suggests that satellite behavior can be as successful as calling (Alexander 1961; Hissmann 1990, 1991; Cade WH and Cade SE 1992; Rowell and Cade 1993; Walker and Cade 2003).

The flexible expression of alternative mating behaviors has the potential to facilitate evolutionary change by creating an environment in which ordinarily maladaptive genetic changes can spread (Baldwin 1896; West-Eberhard 1989, 2003; Yeh and Price 2004; Ghalambor et al. 2007). Examples in which phenotypic plasticity has facilitated rapid evolutionary change in sexually selected traits seem to be rare. For instance, Yeh and colleagues documented a rapid reduction in the white color of the tails of dark-eyed Juncos after their introduction to the University of California, San Diego campus (Yeh 2004; Yeh and Price 2004). The change in morphology was possible because plasticity in breeding season length allowed some females to begin breeding earlier, which aided population growth during the early stages of invasion in an environment that favored lesser white color in the tail (Yeh and Price 2004).

Here, we investigate an example in which satellite behavior may have facilitated the spread of a mutation that eliminated singing ability in a Hawaiian population of Polynesian field crickets (*T. oceanicus*). A recent single-gene mutation that eliminates the calling structures on the forewings of males (file, scraper, and resonating structures) spread through the Kauai population of *T. oceanicus* between the late 1990s and 2003 (Zuk et al. 2006; Tinghitella 2008). The mutation, "flatwing," now affects >90% of males, making them obligately mute, and was favored on Kauai because it protects males from a deadly natural enemy. The fly, *Ormia ochracea* (Tachinidae: Orminii), parasitizes *T. oceanicus* where their ranges overlap in the Hawaiian Islands (Zuk et al. 1993; Lehmann 2003). When gravid, female flies locate cricket hosts by phonotaxis to male calling song (Cade 1975; Zuk et al. 1993) and deposit larvae that will burrow into the male crickets' body cavities where they feed and develop until emerging 7–10 days later (Adamo et al. 1995).

Flatwing males must locate females without the use of their sexual signal. A field experiment suggested that flatwings use satellite behavior to locate females (Zuk et al. 2006). An enhanced phonotaxis response likely moves males into areas where they are more likely to encounter females. Zuk et al. (2006) broadcast *T. oceanicus* calling song from the center of 2-m radius circles in the crickets' natural habitat on 3 Hawaiian Islands, Kauai, and 2 islands where males have normal-winged morphology. They found that more flatwing males on Kauai entered the circles during the playback than did males with normal wing morphology and that flatwings settled in significantly closer proximity to the source of the broadcast song than did normal-winged males. There are 2 alternative explanations for the difference in behavior observed between normal and flatwing male *T. oceanicus*. There may have been preexisting plasticity in male phonotaxis, such that some males behave as satellites under certain conditions, or changes in male behavior may have occurred simultaneously with the changes in wing morphology.

But, which conditions would favor behaving as a satellite if all males are capable of calling? If satellite behavior was preexisting, males may utilize this alternative because they have been unsuccessful in attracting females. It is likely that this sort of behavior would be useful under more common circumstances and not strictly associated with the wing mutation. Some males likely experience low mating success for a variety of reasons—they may be of low quality or located in a poor microhabitat. Males who have not experienced mating success as callers might do better by making the "best of a bad job" as a satellite (Eberhard 1982). A simple decision rule such as "move toward conspecific song when not mated recently" could move an individual into an area of higher local population density where mating may be more common. We suggest that mating experience may be important in this system also because there is a precedent for phonotactic responses of females to depend on recent mating success. In multiple cricket species, female phonotaxis behavior is affected by mating history, with virgin females having enhanced levels of phonotaxis (measured as distance traveled to a broadcast song, speed of response, or response vs. no response) relative to singly or multiply mated females (Koudele et al. 1987; Loher et al. 1993; Prosser et al. 1997; Lickman et al. 1998). This may be the case for males as well.

Here, we investigate variation in male phonotaxis behavior in 4 populations of *T. oceanicus*. We asked 2 questions. First, did satellite behavior predate the mutation to flatwings, providing obligately silent males with an alternative mode of mate location? And second, regardless of wing morphology, is the switch to this alternative mate-searching mode influenced by mating history? Satellite behavior may either have already existed as a behavioral option in the crickets' repertoire (predating the change to flatwing morphology and rendering the wing mutation adaptive) or a series of behavioral changes may have taken place simultaneously with the change in wing morphology. If variation in male phonotaxis behavior predated the mutation, this provides support for the contention that flexible behavior facilitates change in sexually selected traits, thereby speeding the potential rate of evolution. We hypothesized that satellite behavior existed as a behavioral option for *T. oceanicus* prior to the mutation to flatwing morphology because it is less parsimonious to propose that changes in behavior were concomitant with the change in wing morphology and because the reproductive success of males with normal wing morphology is highly variable, with some males likely experiencing little success as callers. If flexibility in male phonotaxis behavior predated the rise of flatwing morphology, we predicted that males of both wing types would have similar phonotaxis behavior, particularly those from the Kauai population and its direct ancestor (see Materials and methods). If, however, satellite behavior is associated with the morphological mutation, flatwing males should behave more like satellites (coming into closer proximity with the source of calling song) than normal-winged males from any population. To address our second question, we manipulated male mating history, hypothesizing that mating experience influences phonotactic behavior and predicting that virgin males would behave more like satellites than multiply mated males, regardless of population of origin and wing morphology.

We first investigated the mate location behavior of males from Hawaii (where the cricket and fly coexist), using the Kauai flatwing population, its direct ancestor, and a third population from the island of Oahu. Satellite behavior is particularly likely to exist in Hawaii because the selective pressure of parasitoid flies may favor a silent strategy. We know, for instance, that selective pressure by *O. ochracea* in Hawaii has favored changes in call structure, the diel distribution of calling, and the response of males to risky calling conditions (Zuk et al. 1993, 1998, 2001; Rotenberry et al. 1996; Lewkiewicz and Zuk 2004). We expanded the study to include a population of *T. oceanicus* from their native range in Australia where selective pressures on sexual signaling are known to differ (the fly is absent in Australia) because satellite behavior may be beneficial in some, but not all locations. We expected the responses of males from Hawaiian and Australian populations to differ because of their alternative environments, with the

behavior of Hawaiian males reflecting their risky signaling environment (this may make satellite-like behavior more prevalent there). This, in turn, would suggest that certain populations are "preadapted" for the type of rapid evolution in sexual signaling observed on Kauai and others are not. As a comparative approach, however, including only one Australian population limits the scope of our conclusions.

MATERIALS AND METHODS

Population origins

Male *T. oceanicus* were isolated from 4 colonies maintained in the laboratory. Two of these are derived from the same location on the island of Kauai; we will refer to these as Kauai and Archival Kauai. Archival Kauai crickets have been maintained in the laboratory since 1992 and were supplemented roughly yearly with the offspring of field-caught females until 2001, the last year in which the population was sampled and no flatwing males found. Archival Kauai has never contained flatwing males. The Kauai colony consists of the offspring of crickets collected from the same field site but was established in 2003 when >90% of males on Kauai were flat winged. All Kauai males used in this study had flatwing morphology. A third Hawaiian population, from the island of Oahu, and a population from the crickets' native range in Eastern Australia (Mission Beach) were also included. All laboratory stocks consist of at least 100 breeding adults at any given time and are regularly (approximately yearly) supplemented with the offspring of field-caught females (except Archival Kauai) to avoid the impacts of inbreeding.

Mating treatments

Males were removed from the large laboratory stocks prior to the penultimate molt and housed in 15-l containers (approximately 30 males per box) with ad libitum access to Fluker's cricket chow or Purina rabbit chow, water, and egg carton for shelter. These boxes were housed in temperature-controlled growth chambers on a 12:12 h light:dark schedule and checked at least 3 times weekly for eclosed adults. On eclosion, males were transferred to smaller containers (540 ml) where they were housed individually and were randomly assigned to 1 of 2 treatments: virgin or mated. Once they had attained an age of at least 5 days after eclosion (when they were sexually mature), each male assigned to the mated treatment was given one opportunity per day to mate with a female from his own population until he had mated exactly 4 times. Sexually mature females supplied to these males were chosen haphazardly from the larger laboratory stocks. A mating encounter consisted of placing the male in an empty container, identical to the one in which he was reared, for up to 2 h with a female. No male mated with a given female more than once. We monitored the behavior of males in a temperature-controlled room set to 25 °C in the dark under red light conditions and noted whether or not the male mated with and transferred a spermatophore to the female before returning him to his individual container. Each male had a maximum of 7 mating opportunities in which to mate 4 times, or he was removed from the study. This was done to minimize age differences between virgin and mated males. Males in the virgin treatment were handled identically (being moved to a "mating container" for 2 h daily) but not given access to females.

Phonotaxis trials

After completing mating treatments, males were tested in single-stimulus phonotaxis trials conducted in a 25 °C room.

The phonotaxis arena was 366 cm long, 36 cm wide, and 30 cm tall, made of pine boards, and covered in flexible clear plastic that could be wiped down between trials. To mimic a more natural substrate, we lined the bottom of the arena with crumpled screening. Calling song of a continuously calling Oahu male recorded in the field at 25 °C was broadcast at 72 dB (at 1 m away) from one end of the arena through a Sony sport CD Walkman and Sony portable speaker (SRS-M30). A phonotaxis trial consisted of placing a male under a small plastic dish at the end of the arena opposite the speaker, beginning the broadcast of calling song, releasing the male, and monitoring his activity for 5 min. After 5 min, we recorded the distance between the male and the speaker to the nearest centimeter (settling distance), removed the male, stopped the broadcast, and wiped down the arena with a 10% bleach solution to eliminate olfactory trails ($n = 57, 61, 55$, and 57 for Kauai, Archival Kauai, Oahu, and Mission Beach, respectively). Additionally, we recorded the time between releasing a male and his first physical contact with the speaker. This was done with all 4 populations but only in half of the trials completed with Kauai and Archival Kauai males ($n = 24, 28, 55$, and 57 for Kauai, Archival Kauai, Oahu, and Mission Beach, respectively). All phonotaxis trials and mating encounters were conducted during the crickets' scotoperiod (dark). A 2-way analysis of variance (ANOVA) with male population, mating history, and their interaction was used to assess whether phonotaxis behavior (contact latency or settling distance) differed across populations or mating treatments. All statistical analyses were performed using JMP 6.0 software (SAS Institute Inc., Cary, NC).

RESULTS

Settling distance

The phonotaxis behavior of males from 3 Hawaiian populations and 1 Australian population of the field cricket *T. oceanicus* showed significant variation overall (Figure 1, Table 1), but Archival Kauai and flatwing Kauai males behaved similarly. Anecdotally, we noted satellite-like behavior in all populations tested (including those from the crickets' native range in Australia); several males from all populations were found within 10 cm of the broadcasting speaker after a 5-min playback (16 of 57 Kauai, 11 of 61 Archival Kauai, 8 of 55 Oahu, and 10 of 57 Mission Beach males). None of these males were displaying aggressive behaviors (for instance aggression song) that would indicate these approaches were intended to establish dominance. We found no significant association between the 4 populations and the frequency of satellite behavior (defined as settling within 10 cm of the broadcasting speaker; $\chi^2 = 3.74$, degrees of freedom [df] = 3, $P = 0.291$). Males from Archival Kauai, Kauai, Oahu, and Mission Beach settled at different distances from the source of broadcast calling song ($F_{3,225} = 6.58$, $P = 0.0003$; parameter estimates ± standard error for Archival Kauai, Kauai, Oahu, and Mission Beach, respectively, were -50.72 ± 13.95, -15.45 ± 14.27, 45.3 ± 14.45, and 20.62 ± 14.27). Pairwise comparisons (Tukey's honestly significant difference technique, $\alpha = 0.05$) revealed that normal wing Archival Kauai males settled closer to the source of broadcast song than did normal-winged males from Oahu and Mission Beach but not significantly closer than flatwing males from Kauai (Table 2). Furthermore, if one divides the phonotaxis arena into 4 equally sized quadrants, the distribution of males among the quadrants is not uniform ($\chi^2 = 18.43$, df = 3, $P = 0.0004$). More individuals settled close to (quadrant 1) and far from (quadrant 4) the broadcasting speaker, as one might expect if males are making a decision to behave like callers or satellites.
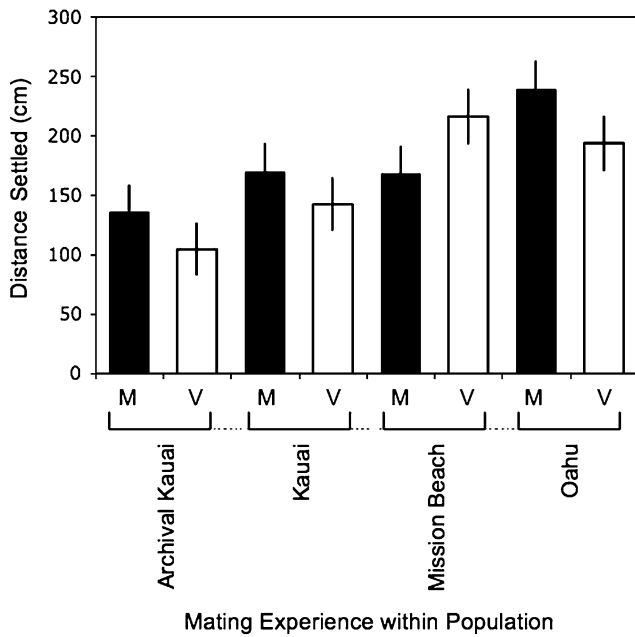
Figure 1
Distance (centimeters) at which males from the 4 tested populations settled from a speaker broadcasting conspecific calling song. V (white bars) = virgin males; M (black bars) = mated males. Values indicated are the mean settling distances (from the speaker, ±1 standard error) after a 5-min playback. Although there were significant among-population differences, males from Kauai and Archival Kauai behaved similarly, supporting the hypothesis that satellite behavior is not strictly associated with nonsignaling males and instead predated the loss of singing ability.

Mating history did not appear to impact male settling distances overall. Multiply mated (178.38 ± 8.22 cm) and virgin (163.99 ± 8.22 cm) male *T. oceanicus* from Hawaii and Mission Beach did not differ in their settling distances ($F_{1,225} = 0.765$, $P = 0.383$), and we found no evidence for an interaction of mating history and population of origin ($F_{3,222} = 1.64$, $P = 0.18$) (Table 1, Figure 1). Further observation of the data

Table 1

ANOVA of 1) the distance at which males settled from the speaker broadcasting calling song and 2) the latency of males to contact the speaker

	df	Sum of squares	F	P
Settling distance				
Population	3	308213	6.67	**0.0002**
Mating history	1	11842	0.77	0.38
Population × mating history	3	75967	1.64	0.18
Error	222	3420403		
Total	229	3816123		
Contact latency				
Population	3	10123	0.62	0.60
Mating history	1	8884	1.63	0.21
Population × mating history	3	735	0.05	0.99
Error	71	385563		
Total	78	407845		

Population and mating history (virgin or mated) were included as main effects (random and fixed, respectively), and the population × mating history interaction term indicates whether the phonotaxis response of males in different treatments varied among the 4 populations. Bold values indicate significance.

Table 2

Mean settling distance (centimeters ± 1 standard error) by population

Population, wing morphology		Mean distance settled (cm)
Archival Kauai, normal	A	120.21 ± 15.54
Kauai, flatwing	A, B	155.39 ± 15.99
Oahu, normal	B	216.36 ± 16.26
Mission Beach, normal	B	191.93 ± 16.52

Levels not connected by the same letter are significantly different (Tukey's honestly significant difference technique, α = 0.05).

revealed that although there was no significant interaction of mating history and population, males from the 3 Hawaiian populations responded to the mating treatment similarly, with virgin males behaving with enhanced phonotaxis relative to mated males. Males from Mission Beach responded with similar magnitude but in the opposite direction, with mated males showing enhanced phonotaxis relative to virgins. These trends, however, were not revealed to be statistically significant, and clearly, as a comparative approach, observing only one Australian population is quite weak. We cannot eliminate the possibility that Mission Beach males are simply not representative of Australian *T. oceanicus* behavior overall. Incidentally, if the Mission Beach population from the unparasitized portion of the crickets' range is removed from the analysis, in a 2-way ANOVA with male population and mating history as main effects, mating history is a marginally significant source of variation in male settling distance ($F_{1,167} = 3.64$, $P = 0.058$).

Latency to contact broadcasting speaker

In the phonotaxis trials, 49.1% of males (79 of 161) from the 4 populations tested contacted the speaker broadcasting *T. oceanicus* calling song (overall). Of those males making contact with the speaker, there were no among-population differences in the latency with which they did so ($F_{3,74} = 0.692$, $P = 0.560$). Virgin males did not contact the speaker more quickly than multiply mated males ($F_{1,74} = 1.578$, $P = 0.213$), and again we found no interaction of the 2 effects ($F_{3,71} = 0.05$, $P = 0.99$; Figure 2, Table 1).

Additionally, there was no relationship between the 2 measures of phonotactic response that we investigated; males who contacted the speaker more quickly did not tend to settle in closer proximity to the speaker broadcasting song ($R^2 = 0.03$, $P = 0.25$). This is consistent with our observation that males frequently left their starting location at one end of the arena and moved toward the broadcast but then contacted the speaker and turned around, continuing to explore the arena space.

DISCUSSION

We hypothesized that satellite behavior existed prior to the mutation to flatwing morphology in Kauai *T. oceanicus*. If this was the case, we expected that the phonotaxis behavior of Kauai flatwing males would not differ from that of normal-winged males, particularly those from the Archival Kauai population (the direct ancestor of the flatwing Kauai population). In phonotaxis trials, we observed some males from all populations showing satellite-like behavior settling in extremely close proximity (<10 cm) to the broadcasting speaker. We found significant among-population variation in the distance at which males from 4 *T. oceanicus* populations settled from the source of a speaker broadcasting conspecific calling song, suggesting that males from some populations are more
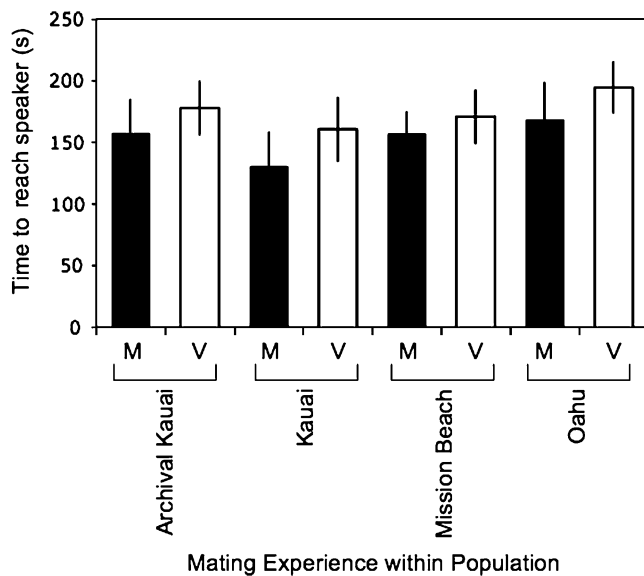
Figure 2
The latency of males (seconds) from the 4 populations to contact the broadcasting speaker after being released at the opposite end of an arena. V (white bars) = virgin males; M (black bars) = mated males. Values indicated are time to reach broadcasting speaker ± 1 standard error. Population of origin and mating history did not influence the latency of males to come into physical contact with the speaker broadcasting calling song.

phonotactic than others. Importantly, however, pairwise comparisons revealed that neither did the phonotaxis behavior of flatwing Kauai males and their direct normal-winged ancestors (Archival Kauai males) differ from one another nor did flatwing behavior differ from that of normal-winged males from Oahu and Mission Beach. That satellite behavior was observed in all 4 populations and males from Kauai and Archival Kauai behaved similarly support our hypothesis that satellite behavior predated the flatwing mutation, accommodating its spread on Kauai by providing obligately silent males with an alternative method of locating mates. We found no evidence that satellite behavior is associated strictly with flatwing morphology (i.e., that the mutation was associated with simultaneous behavioral changes). One might alternatively have hypothesized that flatwing males would show enhanced phonotaxis relative to all other populations because there has been selection (subsequent to the mutation) for increased phonotaxis to aid mate location. Our results are not consistent with this hypothesis, and we suggest that although this may occur at some point in the future, there has likely not been time for the switchpoint between calling and satellite behavior to evolve toward a lower threshold for satellite behavior.

Rapid evolutionary changes in naturally selected traits are common, but the flatwing/normal wing polymorphism is one of few examples of a similarly rapid change in a sexually selected trait (Svensson and Gosden 2007; Zuk and Tinghitella 2008). The paucity of documented examples may in part be due to the suite of traits inextricably tied to sexual signals—the functional complex (Palmer et al. 2007) of signals and associated behavior (Zuk and Tinghitella 2008). Here, we provide one example in which preexisting behavior, satellite, appears to instead make the categorical loss of the sexual signal adaptive by enabling the animals to deal with novelty (Baldwin 1896; Holway and Suarez 1999; Yeh and Price 2004; Zuk and Tinghitella 2008).

One limitation of this study is that the Archival Kauai population is maintained in the laboratory but no longer exists in

the field (having been replaced with the flatwing Kauai population). The Archival Kauai laboratory population has not been supplemented with field-caught individuals since 2001 (the last year in which field studies were conducted and no flatwing males found, Zuk et al. 2006) and may suffer from inbreeding to a greater degree than the other populations studied. Archival Kauai males did show enhanced phonotaxis relative to Oahu and Mission Beach males in terms of settling distance (in pairwise comparisons), but their behavior did not differ from that of flatwing Kauai males. Furthermore, flatwing Kauai males responded in a manner similar to that of Oahu and Mission Beach males, suggesting that the phonotaxis behavior of Archival Kauai males is not particularly unusual.

Second, we hypothesized that mating history affected phonotaxis behavior of male *T. oceanicus*. We predicted that if males experienced poor mating success (as is likely for flatwing males), they would behave more like satellites (showing an enhanced phonotactic response) than recently mated males, regardless of wing morphology or population of origin. Mating history has strong effects on female phonotaxis behavior (virgin females of many species exhibit stronger phonotactic response than do mated females; Koudele et al. 1987; Loher et al. 1993; Prosser et al. 1997; Lickman et al. 1998; Bateman 2001), and some males likely experience low levels of mating regardless of wing morphology. In the 4 populations of *T. oceanicus* we tested, virgin males did not appear to have a greater phonotactic response than multiply mated males (Table 1, Figures 1 and 2). This was true of males with both flatwing and normal-winged morphology.

Interestingly, we found no differences among populations or mating treatments in the speed with which males first contacted the playback speaker, despite highly significant differences in settling behavior. This was consistent with our observation that males frequently approached and/or physically contacted the broadcast but then changed directions and eventually settled away from the speaker. Hissmann (1991) reports a similar behavior in male *Gryllus campestris*; males who were calling themselves frequently approached playbacks but then returned to their burrows. This was interpreted as maintaining an acoustical territorial border or an "exclusive female attraction zone" around the occupied burrow (Simmons 1988). *Teleogryllus*, however, do not occupy burrows, instead calling from tufts of grass or cracks, and our field observations suggest that they interact aggressively when they encounter one another. The absence of variation in latency to contact the song broadcast further supports our contention that satellite behavior is not strictly associated with the morphological change. Rather, males from all tested populations appear to react initially in the same way and then choose a distance at which to settle, which does differ by population. The second choice may arise after individuals have behaved similarly.

On further investigation, we found limited evidence that the behavior of males from Hawaii and Mission Beach, Australia, may differ under alternative mating regimes, so it is possible that differences in the environment (risk of signaling) may be an important contributor to their varied responses. However, because of our weak comparative approach (using only one Australian population), we cannot distinguish between the possibility that the phonotactic responses of Hawaiian crickets are different from those in other portions of the crickets' range (potentially because of the influence of the parasitoid) and the alternative possibility that Mission Beach males are simply not representative of populations from the unparasitized portion of the crickets' range.

Although our data suggest that mating experience is not an important determinant of male mating behavior, other factors may be important in determining how males respond to

conspecific song in Hawaii and elsewhere. Virgin and mated *T. oceanicus* males did not differ significantly in phonotaxis behavior overall (Figures 1 and 2). A fundamental difference between males and females may contribute to the absence of an effect of mating experience on male phonotactic behavior. Females receive enough sperm in one mating to successfully fertilize all their eggs. They may mate multiply to secure direct or genetic benefits or both (Andersson 1994; Jennions and Petrie 2000). Multiple mating by males, however, is adaptive because it continues to increase reproductive success far beyond the point of diminishing returns for females (Bateman 1948). Mated males, therefore, may not reduce their phonotaxis responses even after mating multiple times because it is not beneficial to do so, unless mating or mate-searching behavior are extremely risky.

Additionally, the observation that a given male may perform calling and satellite behavior during the course of a night suggests that a more immediate proximate cue may be responsible for the switch from calling to satellite behavior (Rowell and Cade 1993; Hack 1998). Empirical and theoretical work with field crickets suggest that population density, sex ratio, presence of parasitoid flies, and the proportion of satellites in the population are important determinants of the relative success of calling and satellite behaviors (Rowell and Cade 1993; Walker and Cade 2003). In some organisms, alternative mating behaviors are more common in locations where the influences of natural and sexual selection on sexual signaling conflict, such as when males must balance attracting females with attracting enemies. For instance, in guppies, less visually conspicuous gonopodial thrusts are favored over the more conventional displays in areas where risk of predation is high (Godin 1995). This may be the case for field crickets as well (Cade 1979), with the threshold for switching to satellite behavior being shifted in areas where parasitoid flies are attracted to signaling males. Selection by *O. ochracea* seems to have favored a shift in the diel distribution of calling in Hawaiian *T. oceanicus* populations, such that males do not call in the early evening when flies are active (Zuk et al. 1993). Under this hypothesis, noncalling males would be more prevalent in Hawaii and satellite behavior more common there. The acoustic environment likely informs crickets about such things as the local population density, and males may also use such cues to determine when to pursue alternative mating behaviors. Future work should focus on investigating the contributions to variation in male mating behavior across the crickets' range with attention to establishing these patterns in many populations.

FUNDING

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