Preexisting behavior facilitated the loss of a sexual signal in the field cricket *Teleogryllus oceanicus*

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Behavioral preadaptations can provide an accommodating environment in which novel morphological characters may be selected. A very recent morphological mutation, *flatwing*, has caused the loss of male song in field crickets (*Teleogryllus oceanicus*) from the Hawaiian island of Kauai. Previous studies in this and related species have shown that females require male courtship song to mount males, but flatwing *T. oceanicus* males still achieve matings. Females from Kauai may have a relaxed requirement for male courtship song, or flatwing males may compensate for their inability to sing by altering other courtship behaviors. We tested whether male courtship and female responses to male courtship were preadapted in a way that facilitated the spread of the male wing mutation or if parallel changes in male courtship and female responses accompanied the mutation. We performed mating trials in 2 captive-bred populations to assess how mating behavior varied depending on the presence or absence of courtship song playback. The first was an ancestral population from Kauai established prior to the emergence of the flatwing mutation, and the second was derived from Kauai after the mutation became prevalent. Mating behaviors did not differ qualitatively or quantitatively between the ancestral and current populations, and females from both accepted males for mating in the absence of courtship song. Our results provide direct evidence that a mechanism allowing flatwing males to mate with females was in place before the mutation actually arose on Kauai and demonstrate how preexisting behavior facilitated the rapid spread of a novel morphological mutation. *Key words:* behavioral preadaptation, courtship song, field cricket, playback experiment, rapid evolution, *Teleogryllus oceanicus*. [*Behav Ecol* 19:202–207 (2008)]

Behavioral attributes have long been recognized to influence the evolution of novel morphological characters (Baldwin 1896; Mayr 1974; West-Eberhard 1989; West-Eberhard 2003; Yeh and Price 2004). Because of its crucial role, some authors have suggested that behavior influences the evolvability of certain groups: the existence of complex behavioral repertoires may increase the rate at which favorable genetic changes become established (Wcislo 1989). However, a key problem in studying the influence of behavior on morphological adaptations is that ancestral behavioral states can be difficult to infer (Wcislo 1989; Baum and Larson 1991). Directly demonstrating how behavior in an ancestral population could facilitate the emergence of a novel morphological trait is also challenging because major evolutionary changes infrequently take place on a contemporary timescale. However, a very recent mutation in wing morphology causing the loss of a sexual signal—song—in a population of the field cricket *Teleogryllus oceanicus* provides a unique opportunity to examine precisely how behavior associated with courtship and mating may have accommodated the emergence and spread of a novel morphological change.

Male field crickets (Gryllidae) typically produce 2 types of songs in the context of mating. Calling song attracts phonotactic females from long distances, whereas courtship song is produced only when a male and female are in close proximity to one another (Alexander 1962). Antennal contact between the pair involving chemosensory cues is required to initiate a stereotyped series of courtship events (Balakrishnan and Pollack 1997). At this point, the male produces a species-specific courtship song, and if the female is receptive she will mount him (Burk 1983). Copulation is complete when the male successfully transfers a spermatophore to the female. Male coercion in gryllids is impossible because a male cannot transfer a spermatophore unless he has been mounted by a female. Inducing a female to mount has been thought to depend crucially on the ability of a male to produce the close-range courtship song to release female mounting behavior (Huber 1955; von Hörmann-Heck 1957; Alexander 1961; Crankshaw 1979; Burk 1983; Adamo and Hoy 1994; Balakrishnan and Pollack 1996).

The intricate sequence of events comprising cricket courtship and mating has been recently disrupted in a unique Hawaiian population of *T. oceanicus*. On the island of Kauai, a single-locus, sex-linked mutation affecting male wing morphology has arisen and spread over fewer than 20 generations, apparently in response to selective pressure from an acoustically orienting parasitoid fly, *Ormia ochracea* (Zuk et al. 2006). Ordinarily, a toothed file on the underside of the right wing is drawn across the top of the plectrum, or scraper, on the upper surface of the lower wing during elytral closing, causing resonating structures on the wings to vibrate and produce sound (Ewing 1989). However, males in Kauai that carry the mutation develop wings that almost completely lack all specialized structures involved in the production of sound (Zuk et al. 2006). These "flatwing" males can still make stridulatory motions with their wings, hereafter referred to as "stridulation", but are unable to produce any sound. Silent flatwing males appear to act as satellites (Cade 1979, 1980) to the remaining callers, intercepting phonotaxing females and mating with them (Zuk et al. 2006).

Once in close proximity to a female, however, how do silent flatwing males achieve successful matings if they cannot produce a courtship song? Females clearly accept males that do not produce a courtship song; otherwise, the flatwing mutation would have been swiftly counterselected to extinction. Here we investigate whether relaxation in the courtship song

requirement of females preceded or accompanied the flat-wing mutation itself. We used a laboratory colony of crickets established from the Kauai population prior to the mutation's emergence ("ancestral Kauai" [AK]) and a laboratory colony derived several years after its emergence ("current Kauai" [CK]). The flatwing mutation originated in Kauai. Males from other Pacific island and Australian populations remain normal, although a small number of flatwing males have appeared on the neighboring Hawaiian island of Oahu (Zuk et al. 2006). Therefore, we have focused the present investigation on the behavioral properties of crickets from Kauai that may have facilitated the rapid spread of the flatwing morphology within that particular population.

First, both male courtship behavior and female responses to male courtship may have been preadapted in the ancestral population in a way that facilitated the spread of the flatwing mutation. Females in the ancestral population might mount males in the complete absence of song, or be induced to mount a silent male if the pair is situated within acoustic range of another singing male, or both. In this case, we predicted that both males and females in the AK and CK populations would show similar behavioral responses to male courtship playbacks, namely, that courtship song would not be strictly required for female mounting in either population and also that both the likelihood and timing of male stridulation and spermatophore transfer would not differ between the populations. Alternatively, pleiotropic effects or simultaneous, independent mutations may have accompanied the male flatwing mutation, affecting male courtship or female response to male courtship. Female behavior may have shifted so that courtship song is no longer required for female mounting in the current population, and females will readily mate with silent flatwing males. Additionally, male mating behavior may be altered in the current population, compensating for the loss of song. For example, males may transfer spermatophores more quickly once they are mounted. Under this scenario, we predicted that females would require courtship song for mounting in the AK population, as has been documented in other studies (Crankshaw 1979; Burk 1983; Adamo and Hoy 1994; Balakrishnan and Pollack 1996) but that this requirement would be reduced or altogether eliminated in the CK population.

To test these hypotheses, we performed mating trials using females and muted or flatwing males under 2 conditions: silence and with courtship song playback. This allowed us to compare the effects of courtship song and its absence on the tendency of crickets to perform particular mating behaviors such as stridulation, female mounting, and spermatophore transfer in both the AK and CK populations. We also investigated the latency of males to stridulate, of females to mount, and of males to transfer a spermatophore. Our results reject the hypothesis that gross changes in mating behavior accompanied the male-wing mutation in favor of the idea that behavioral preadaptation contributed to the rapid spread of the flatwing morphology in males from Kauai.

METHODS

Colony origin and rearing

We used 2 laboratory populations of *T. oceanicus* originally derived from the Hawaiian island of Kauai. One of these populations (AK) was established prior to the emergence of the flatwing mutation in 2003 and maintained at a large population size (between 100 and 300 individuals) to reduce the effects of inbreeding. There have never been flatwing males in AK, and all AK males have normal wing morphology. The other population was established in 2006 from the same location on Kauai (CK). To avoid maternal effects, we used the F$_2$ generation of wild crickets collected in May of 2006. More than 90% of males on Kauai are now flatwings (Zuk et al. 2006), and the same proportion in CK were flatwings when we ran our experiments. We used normal males from AK and flatwing males from CK during mating trials.

Crickets were reared in 15-L containers at 25 °C on a 12:12 photo-reversed light:dark cycle. Fluker's cricket chow, Purina rabbit chow, and water were provided ad libitum. To reduce age variation, we separated crickets into same-instar equal-density cohorts of 40 per box when sex differences became apparent. These were maintained until the crickets completed their final moult (all enclosed within ca. 1 week of each other). Females and males were then transferred to individual 118-mL containers with food, a water vial, and egg carton for shelter for 1 week.

Prior to transferring AK males, we removed the plectrum on the lower left wing using dissecting scissors. Removal of the plectrum silences males with normal wing morphology because the stridulatory pegs on the underside of the top wing no longer engage with any structure on the lower wing during wing closure. Manipulation in this manner has no discernable effect on males' ability or tendency to move their wings (Bailey N, personal observation), and was necessary to ensure that mating behaviors in AK and CK were observed under precisely the same conditions (i.e., males from both populations were able to make stridulatory motions with their wings but did not produce any sound). Thus, female responses to males during mating trials would only be influenced by the artificial playback, and not the ability of AK males to actually produce sound when they stridulated, allowing us to draw a direct comparison between the behaviors of AK and CK females and AK and CK males.

Courtship song recording

Courtship song in *T. oceanicus* consists of a short chirp containing several pulses of increasing amplitude followed by a long trill-like element (Balakrishnan and Pollack 1996). Courting males from AK were digitally recorded in the laboratory with a Sennheiser ME 66 directional microphone with a K6 power supply. We used Raven v. 1.2 software to construct a representative courtship song for playback by extracting and altering the number and spacing of pulses in the chirp and trill elements of the previously recorded song. The total song duration was 3.874 s. The durations of the chirp, the interval between the chirp and trill, and the trill were 0.514, 0.084, and 3.276 s, respectively. The mean durations of the chirp pulse, chirp pulse interval, trill pulse, and trill pulse interval were 0.028, 0.042, 0.020, and 0.012 s, respectively. These values are comparable to average courtship song parameters found in another Hawaiian population of *T. oceanicus* (Zuk M and Scott SP, unpublished data) and in an Australian population (Tregenza et al. 2006). The carrier frequency of the courtship song was 4.6 kHz.

Mating trials

After 7 days of isolation, males and females were paired in cylindrical 540-mL containers 9 cm in diameter. Males and females from the same population were tested together. We performed mating trials during the crickets' dark cycle in a dimly lit room with no natural sunlight between 20 and 25 °C. All behavioral observations were made visually and noted on data sheets. Starting from when the male and female were placed in the container together, we noted the amount of time it took for males to start stridulating and for females to mount males. We also recorded how long it took males to transfer a spermatophore after having been mounted and

whether the male or female failed to perform one or more of these actions. Observations began without delay after a male and female were placed together in a chamber because some pairs began courtship behavior almost immediately. Pairs of crickets were allowed 10 min to complete a mating trial and were used only once.

In the control condition, mating trials were carried out in silence. In the experimental condition, the previously synthesized courtship song was broadcast from a Benwin BW FX2-3D speaker suspended above the male and female. Song was played continuously on a Sony Sport CD walkman. The sound pressure level of a courting *T. oceanicus* male at the position of the male himself likely exceeds 90 dB (Balakrishnan and Pollack 1996). To mimic a situation in which a female encounters a satellite male that is some distance from a courting male, we calibrated the sound pressure level of our playbacks to 70 dB at the position of the crickets using a Precision (type 2235) sound level meter.

Forty-two AK mating pairs were tested without song, and 44 were tested with song. Twenty-nine CK mating pairs were tested without song, and 28 were tested with song. We measured the effects of treatment (song or no song) and population (AK or CK) on whether or not 1) males stridulated, 2) females mounted males, and 3) males transferred a spermatophore to females, and the latency until each behavior occurred. It was important to assess not only tendencies of crickets to perform a particular behavior but also the time it took them to do it, as population differences in the latter would also lend support to our alternative hypothesis. We analyzed frequency data using 3-way G-tests (Sokal and Rohlf 1969) and time data using general linear models (GLMs). Time data were $\log_{10}$ or square root transformed to improve normality before inclusion in GLMs.

RESULTS

Frequency of mating behaviors

The likelihood of mating behaviors occurring varied by treatment but not the population from which the crickets were derived (Table 1, Figure 1). When song was played, stridulation was significantly less likely to occur, whereas mounting and spermatophore transfer were significantly more likely to occur (Table 1, Figure 1). Nonsignificant interaction terms in the G-tests indicated that AK and CK did not differ in any of the 3 behavioral responses to song treatment (Table 1). In other words, exposing pairs of crickets to artificial courtship song had a considerable effect of equal magnitude and direction in AK and CK on male stridulation, female mounting, and spermatophore transfer (Table 1, Figure 1).

More than 40% of cricket pairs successfully mated in silence, regardless of their population origin, but exposing pairs to artificial courtship song increased mating frequencies to approximately 70% (Figure 1). The restorative effect of artificial courtship song was driven by females' increased tendency to mount males when courtship song was present, as opposed to an increased tendency for males to produce and transfer a spermatophore when song was present. Approximately 55% of females in both populations mounted males in the absence of song, compared with nearly 90% that mounted when exposed to courtship song playback (Figure 1). Most males (77%) that were mounted transferred a spermatophore successfully, and the likelihood that a mounted male would transfer a spermatophore did not vary by treatment or population (G-test: $G_4 = 2.12$, $P = 0.713$). More than 80% of males stridulated when song was absent, whereas only half stridulated when song was present (Figure 1). When males

Table 1

3-Way G-tests of the proportion of cricket pairs exhibiting each mating behavior

	Degrees of freedom	G	P
Stridulation			
3-Way independence	4	17.76	**<0.001**
Population	1	0.39	0.532
Treatment	1	15.54	**<0.001**
Population × treatment	1	1.79	0.181
Mounting			
3-Way independence	4	20.19	**<0.001**
Population	1	0.11	0.740
Treatment	1	18.64	**<0.001**
Population × treatment	1	1.39	0.239
Spermatophore transfer			
3-Way independence	4	10.55	**0.032**
Population	1	0.35	0.553
Treatment	1	9.79	**0.002**
Population × treatment	1	0.35	0.554

Results are presented separately for male stridulation, female mounting, and male spermatophore transfer. Population (AK or CK) and treatment (song or no song) are included as main effects, and the population × treatment interaction term indicates whether the response to the different treatments varied between the 2 populations. The 3-way independence term indicates the overall G-value for each test. Significant P values are indicated in boldface.

stridulated, they produced no sound either because we had removed their plectrums or they were flatwings. The increased tendency for males to stridulate under silent conditions did not compensate for the decreased tendency of females to mount them.

Many females (70%) successfully mounted and received a spermatophore from nonstridulating males. Females were more likely to mate with a nonstridulating male if courtship song was present (G-test: $G_1 = 5.66$, $P = 0.017$). Similarly, females were significantly more likely to mount a nonstridulating male if courtship song was present (G-test: $G_1 = 4.548$, $P = 0.033$), but spermatophore transfer did not appear to differ between the song treatments. Small sample sizes precluded us from statistically analyzing data for nonstridulating mounted males. However, only 5 of these males (14%) did not transfer spermatophores, and they were evenly distributed throughout populations and treatments. We were unable to determine whether males or females controlled the breakup of the mounted pair. Despite the fact that females did not mount or mate nonstridulating males as readily in the absence of song, 7 females mounted nonstridulating males in the absence of song, and 5 of these pairs ultimately mated. As before, mating behavior in pairs comprised of nonstridulating males did not vary by population (G-tests: all $G_1 < 0.618$, all $P > 0.431$).

Timing of mating behaviors

Overall, male crickets took longer to begin stridulating in the "no song" treatment group (GLM: $F_{1,89} = 4.86$, $P = 0.030$). However, AK males started to stridulate sooner in the "song" treatment, whereas there was no difference between treatments in the time it took CK males to begin stridulating (GLM: $F_{1,89} = 13.94$, $P < 0.001$) (Figure 2). Female crickets took longer to mount males when song was absent (GLM: $F_{1,101} = 7.55$, $P = 0.007$) regardless of what population the pair was from (GLM: $F_{1,101} = 0.19$, $P = 0.663$) (Figure 2).
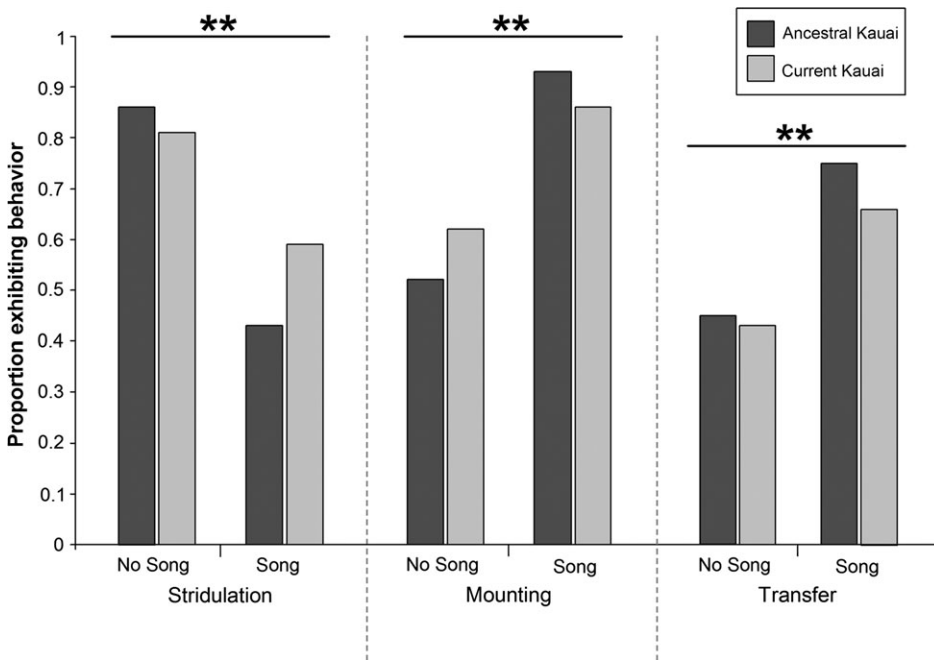
Figure 1
Frequency of mating behaviors across song treatment and populations. The double asterisks indicate significant differences ($P < 0.01$) in the frequency of mating behaviors between the 2 treatments (no song vs. song). Differences between populations were not significant (see Table 1).

Finally, the time between mounting and spermatophore transfer did not vary by population or treatment (GLM: all $F_{1,77} < 0.97$, all $P > 0.327$).

DISCUSSION

Overall, male courtship behavior and female responses did not differ qualitatively or quantitatively between AK and CK. These results do not support the idea that the flatwing mutation was associated with simultaneous changes affecting male or female mating behavior and instead favor the hypothesis that on Kauai, male courtship and female responses to male courtship were preadapted in a way that facilitated the spread

of the male flatwing mutation. No substantial changes in male behavior during courtship seem to have accompanied the flatwing mutation. It therefore seems unlikely that flatwing males concomitantly developed an enhanced ability to induce female mounting behavior in the absence of courtship song. Female responsiveness to courting males was consistent across both populations. The fact that courtship song playbacks increased the tendency of females to mount, and therefore increased overall mating frequency of randomly paired crickets, is consistent with earlier findings (Burk 1983; Liebersat et al. 1994; Balakrishnan and Pollack 1996). This effect has traditionally been examined in the context of the function of courtship song as a releaser of female mounting behavior
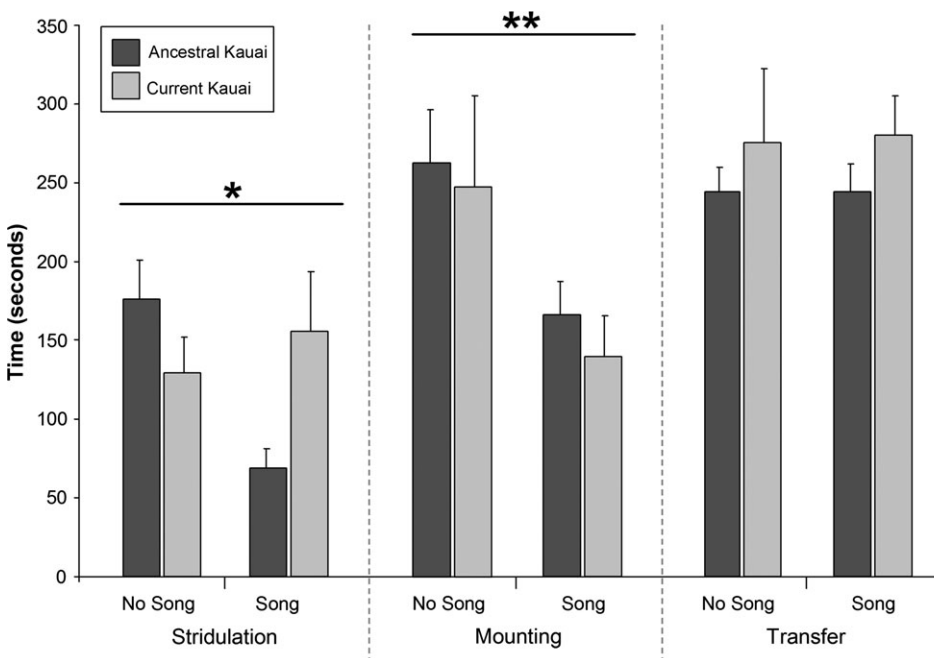

Figure 2
The time until each mating behavior occurred across song treatments and populations. Error bars indicate standard error (SE), and asterisks indicate significant differences between treatment groups (*$P < 0.05$, **$P < 0.01$). Differences between populations were not significant (see Results).

(Walker and Masaki 1989), but it also has clear implications for the evolution of satellite strategies. On Kauai, a female tendency to mate both in the complete absence of song and in the presence of reduced-intensity courtship song has provided a behavioral environment that facilitated the spread of the silent flatwing mutation in males, which would have been swiftly counterselected otherwise.

Courtship song was not necessary for successful mating, as more than 40% of males from both AK and CK successfully transferred a spermatophore to a female in silence. Female mounting rates in the absence of song were even higher, exceeding 50% in both AK and CK. This contrasts with previous studies of *T. oceanicus* and other gryllids, which concluded that courtship song is necessary for successful mating (von Hörmann-Heck 1957; Crankshaw 1979; Burk 1983; Balakrishnan and Pollack 1996). Liebersat et al. (1994) and Balaskrishnan and Pollack (1996) noted that wing removal in *T. oceanicus* does not entirely preclude mounting but only severely reduces its likelihood. However, the mating rate of silenced males in our study far exceeded the roughly 10% mating rate of silenced males found by Liebersat et al. (1994) and 16% mounting rate of silenced males found by Balakrishnan and Pollack (1996). Direct comparisons between these studies and ours should be made with caution because of several methodological differences such as the surgical procedures used to silence males and the sizes of mating arenas. However, it seems unlikely that the size of the mating arena had a substantial impact on the tendency of females to mount and mate in this study because silent flatwing males and females from Kauai mate at the same rate when tested in larger arenas (17 × 11 cm) (Tinghitella R, personal communication). Previous researchers silenced males by completely removing both elytra (Liebersat et al. 1994; Balakrishnan and Pollack 1996). Differences in the surgical procedures used to mute males could account for the discrepancy in female mounting rates if female mounting is influenced by vibrations or pheromonal signals arising from elytral movement. However, we are unaware of any data to support either scenario, as males are liable to produce vibrations even when their wings are completely removed (Balakrishnan and Pollak 1996), and chemosensory cues are likely to be transmitted through direct antennal contact (Balakrishnan and Pollak 1997).

Although the proportion of matings occurring in the absence of song may have been underappreciated in the past, our results suggest that mounting in the absence of song was of singular importance during the rapid spread of the flatwing mutation on Kauai. Balakrishnan and Pollack (1996) also found that female mounting could be restored to normal levels by playing back calling and aggression songs during mating trials, which suggests a mechanism by which silent flatwing males induce females to mount. Flatwings apparently act as satellites to the few remaining callers in the population (Zuk et al. 2006), and the calling song of a nearby male may be sufficient to induce a female to mount with a flatwing satellite. Additionally, olfactory signals transmitted during courtship may compensate for the lack of acoustic cues. Cuticular contact pheromones have been characterized in field crickets (Tregenza and Wedell 1997) and are important in sex recognition and the detection of social dominance (Kortet and Hedrick 2005). In *Acheta domestica*, odor cues are important mediators of phonotaxis and other behaviors associated with reproduction (Koudele et al. 1987). Chemical signaling through antennation is known to play an important role in the courtship repertoire of *T. oceanicus* (Balakrishnan and Pollak 1997), and females may rely more heavily on olfactory cues to evaluate a potential mate when courtship song is unavailable. Regardless of the mechanistic basis of the preadaptation, the key point is that the dynamics of courtship

behavior and male wing morphology did not undergo a synchronized change. The mechanism allowing Kauai females and silent flatwing males to successfully mate was in place before the flatwing mutation actually appeared.

Behavior can play a role in the evolution of novel morphologies in several ways. For instance, changes in a behavioral repertoire may provide new selective pressures favoring morphological novelty (i.e., behavior driving morphological evolution). Alternatively, preexisting behaviors may allow the establishment of morphological novelty driven by separate selection pressures (i.e., behavior facilitating morphological evolution). The courtship dynamics and morphological change we have documented in *T. oceanicus* are an example of the latter. A proposed sequence of events describing the rise and spread of the flatwing mutation follows. First, alternative mating tactics, particularly male satellite behavior, have been demonstrated in a number of species (Alexander 1961; Cade 1979, 1980, 1981; Rowell and Cade 1993) and likely existed in *T. oceanicus* populations prior to their exposure to the acoustically orienting parasitoid *O. ochracea* (Zuk et al 2006). The *T. oceanicus* population on Kauai has always harbored the highest number of infested males compared with other parasitized populations (Zuk et al. 1993; Zuk et al. 1998), and within it, a massive morphological change—the alteration of wing structure—arose and spread nearly to fixation in fewer than 20 generations (Zuk et al. 2006). Stereotyped male courtship behavior and female responses to it predated the wing mutation and persisted in the population after it arose. We propose that the combination of female readiness to mount in silent conditions, combined with a tendency for flatwing satellite males to be necessarily within acoustic range of calling males (Zuk et al. 2006), accommodated a novel morphology driven by parasitoid selection pressure.

Our data reveal several other interesting aspects of courtship behavior in the AK and CK populations. Males from AK did not produce sound during stridulation because we altered their wings, but flatwing males from CK did not produce sound because their wings lack sound-producing structures to begin with. Nevertheless, flatwings still stridulate despite the energetic costs involved (Walker and Masaki 1989; Hack 1998). The tendency of males from both AK and CK to stridulate was similarly affected by courtship song playback, with males less likely to stridulate at all during their encounters with females if courtship song was present. Previous work has established that males avoid calling during periods of high parasitoid activity in parasitized populations of *T. oceanicus*, whereas unparasitized populations show no shifts (Zuk et al. 1993). Additionally, selection from *O. ochracea* may drive alterations in certain temporal components of male-calling song (Zuk et al. 1998). Parasitism risk affects male calling dynamics in a variety of species, including katydids (Bellwood and Morris 1987; Schul and Patterson 2003), frogs (Ryan 1995), birds (Gill and Sealy 2004), and other acoustically signaling animals (Zuk and Kolluru 1998). The ears of gravid *O. ochracea* females are highly sensitive to sounds within a certain frequency (about 5 kHz), and flies phonotax toward calling male crickets with deadly accuracy (Robert et al. 1992, 1994). Although the attractive properties of courtship song to *O. ochracea* females have not been investigated, our results are consistent with the idea that males reduce predation risk by refraining from producing courtship song when song from nearby males is audible. Because the song of a nearby male is apparently sufficient to restore female mounting to levels observed when a male himself sings, males may enjoy an advantage by facultatively refraining from singing. It is intriguing that this behavior has been retained by flatwing males. In the future, selection against energetically expensive elytral movement (Walker

and Masaki 1989; Hack 1998), plus the absence of sexual selection on song, might be predicted to eliminate stridulatory behavior in flatwing males altogether.

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