Obligate, but not facultative, satellite males prefer the same male sexual signal characteristics as females

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Signalling is energetically expensive and increases the risk of predation and parasite infection. To balance the costs and benefits of mate attraction, individuals may adopt an alternative mating strategy such as satellite behaviour, in which nonsignalling males will settle near signalling males and attempt to intercept approaching females. While many suggest that alternative strategies are 'making the best of a bad job', little research has examined whether satellites, particularly obligate satellites, have the potential to increase their mating success by preferentially targeting more attractive signallers. Using the Pacific field cricket, *Teleogryllus oceanicus*, we tested the hypothesis that males are more likely to act as satellites to signalling males with particularly attractive songs, as these callers are likely to attract the most females. In this species, a novel male wing mutation, 'flatwing', renders some males unable to call. Flatwings are obligate satellites, while nonmutated, normal-wing males switch between calling and satellite strategies. We presented males with calling song models varying in the percentage of long-to-short chirps, a characteristic important in female choice. As was shown for females in previous work, flatwings exhibited a strong preference for calling songs composed of 60% long chirp. Normal wing males did not prefer any particular calling song model. Our results lead to the paradoxical conclusion that males with highly attractive songs may not have the highest mating success. Such male preference for male sexual signals may oppose selection by females and increase competition between signalling and satellite males. This could potentially slow the rate of male trait evolution and influence the evolution of male competition.

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Many animals signal to attract mates (Bradbury & Vehrencamp, 2011), but signalling can be energetically expensive (Stoddard & Salazar, 2011) and can render individuals vulnerable to increased predation by unintended receivers (Zuk & Kolluru, 1998). To ameliorate the costs of attracting mates, individuals may adopt an alternative mating strategy, such as satellite behaviour, in which nonsignalling males will settle near signalling males and attempt to intercept approaching females (Shuster, 2010). This strategy allows individuals to increase their reproductive success, while decreasing the likelihood of encountering predators or parasites (Shuster, 2010).

Satellite behaviour has been documented in a number of anurans and insects (Gerhardt & Huber, 2002; Leary & Harris, 2013), birds (Küpper et al., 2016; Lank et al., 2002) and fishes (Tudor & Morris, 2011; reviewed in Neff & Svenson, 2015). It remains unclear, however, whether the calling and satellite strategies have equal fitness payoffs. Furthermore, the extent to which satellite males differ among themselves with regard to mating success, based on the signalling male they associate with, remains relatively unknown. Because the satellite strategy involves intercepting females that approach signalling males, it stands to reason that if a satellite male is to increase the number of females he mates with, he must increase the number of females he encounters near a signalling male.

But how might satellite males increase the rate at which they encounter females given that this strategy relies on other, signalling, males? To answer this question, Waltz (1982) proposed the 'satellite threshold model' in which he predicted that satellite males should concentrate on areas most attractive to females. Thus, if a male engages in satellite behaviour with a highly attractive calling male, he is likely to encounter and mate with more females than if he acts as a satellite to a less preferred male. However, this hypothesis predicts that satellites adopt this

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alternative tactic based on the attractiveness of the area that a male is occupying (Waltz, 1982). In a similar vein, the 'relative attractiveness hypothesis' predicts that males adopt a satellite tactic when the attractiveness of a nearby signalling male exceeds their own attractiveness (Berec & Bajgar, 2011; Brepson, Troïanowski, Voituron, & Lengagne, 2012; Castellano, Marconi, Zanollo, & Berto, 2009; Humfeld, 2008). Often studies of satellite behaviour are interested in the rules governing tactic expression in systems where males can switch between various alternative mating strategies throughout their lives. What happens when a tactic is fixed and males must engage in satellite behaviour to attract mates?

Furthermore, many of these studies are examining how males group, as in lekking or chorusing species. Instead, we want to understand what happens when individuals show a preference for particular signals that can have a direct impact on their reproductive success. Here we want to address whether an underlying preference exists with the assumption that such a preference has the potential to increase the reproductive success of satellites.

The Pacific field cricket, *Teleogryllus oceanicus*, provides a unique opportunity to test how the 'decision rules' regarding satellite behaviour are affected by a male's reliance on this alternative strategy. Like other field crickets, *T. oceanicus* males produce a long-range calling song by rubbing specialized forewing structures together. This song attracts females for mating but can also attract predators and parasites. In populations of *T. oceanicus* introduced to the Hawaiian Islands, calling song attracts an acoustically orienting parasitoid fly, *Ormia ochracea*, that parasitizes and kills calling males (Otte, 1994; Zuk, Simmons, & Cupp, 1993). Male crickets appear to cope with the costs of signalling by engaging in satellite behaviour, whereby some males will forgo calling, settle near a calling male and intercept approaching females (Zuk, Simmons, & Rotenberry, 1995).

More recently, in the Hawaiian populations of *T. oceanicus*, a novel male morph, 'flatwing', has become established. Flatwing males have a genetic mutation that greatly reduces their forewing structures, rendering them unable to call (Tinghitella, 2008; Zuk, Rotenberry, & Tinghitella, 2006). Instead, these flatwing males coexist with and capitalize on the calling song produced by non-mutated, normal-wing males as a means of achieving reproductive success (Zuk et al., 2006). While flatwing males must always rely on satellite behaviour, normal-wing males engage in a facultative satellite behaviour, switching between calling and satellite strategies throughout their lives. Given the risk of calling in these populations, both flatwing and normal-wing males may adopt satellite strategies. However, the importance of this strategy for reproductive success differs depending on whether a male has the option of calling.

Here we test the hypothesis that satellite males may increase their chances of acquiring mates by preferentially settling near more attractive signalling males. We sought to examine whether males show a preference, the way that females do, for certain signal characteristics, with the assumption that this would allow satellites to access more females and thereby increase their reproductive success. We suggest that if males are capable of discriminating among signalling males, then satellite behaviour could be favoured if satellites obtain fitness that is equal to or greater than that of signalling males. For obligate satellites, discriminating among different signal qualities could make the difference between never mating and mating with multiple females. Additionally, if satellites are shown to discriminate, this can have implications for the success of signallers such that the fitness of a signalling male will depend on the likelihood of attracting females for mating and the likelihood of attracting rival males. If a

male is deemed to have an attractive song by both females and rival males, then his mating success may decrease due to the presence of satellite males near him. Because flatwings are obligate satellites, this study can also help us understand how a drastic change in reproductive morphology (i.e. a change in the underlying wing morphology necessary for sexual signalling) can be accommodated through an alternative strategy. In this case the alternative strategy has become the primary strategy for a subset of males, seemingly with little decrease in reproductive fitness that might be expected if males are 'making the best of a bad job' (West-Eberhard, 2003).

To test the hypothesis that satellites of both male morphs discriminate among calling males, we examined how males responded to different calling song models in the laboratory. Male *T. oceanicus* produce a two-part calling song of long and short chirps (Fig. 1; Bailey & Zuk, 2009). The proportion of long to short chirps has been shown to be particularly important in the context of female mate choice (Fig. 1; Simmons, 2004; Simmons, Zuk, & Rotenberry, 2001), with females responding fastest to calling song models with 60% long chirp (Bailey & Zuk, 2008). This female preference is likely influenced by selection on the duration of long chirps by *O. ochracea* (Simmons, 2004) where the probability of becoming infested is positively correlated with the duration of long chirps in the calling song (Zuk et al., 1998). Here, we examined how males respond to different calling song models. Using playback experiments in the laboratory, we tested whether males would exhibit a preference, measured in terms of response time, to the 60% long chirp song model (Bailey & Zuk, 2008). We predicted that both male morphs would show a preference for the 60% long chirp song model, although we expected that flatwings might exhibit a strong preference because they are obligate satellites. We also measured the amount that males moved around in the testing arena. We predicted that males would move around in the testing arena less when they responded positively to the playback speaker, relative to when they responded negatively. Males that hear unattractive songs in the wild probably move about until they find a male producing an attractive call. Thus, we expected that males would move around more in the testing arena when they responded negatively to a calling song model.

METHODS

Study Organism

We used *T. oceanicus* males from the Hawaiian island of Oahu. This island has a roughly equal proportion of normal-wing to flatwing males (Pascoal et al., 2014), meaning that males probably use
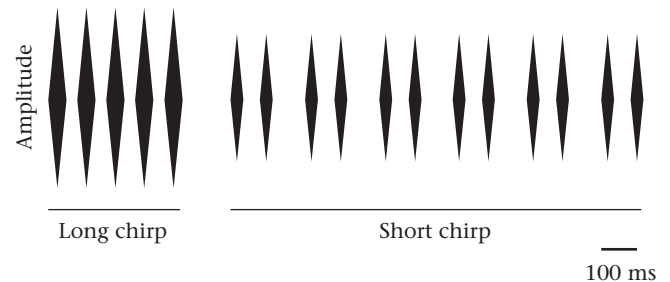

Figure 1. Oscillogram of *T. oceanicus* calling song from Bailey and Zuk (2009). Each vertical black line represents a pulse in the cricket song. Males produce a long-range song by rubbing specialized wing structures together. The song consists of two discrete phrases: the long chirp, which includes three to eight sound pulses, followed by a series of short chirps, each with two sound pulses.

a satellite strategy to find mates. A laboratory population of *T. oceanicus* was originally established using approximately 100 crickets collected from the University of Hawaii- Manoa campus in 1993 and 1994 (Zuk et al., 1995). Each year the laboratory population is supplemented using offspring of wild-caught females from Oahu to maintain a minimum of 100 breeding individuals in the colony at all times. We reared crickets in incubators (Caron Insect Growth Chambers model 6025, Caron Products, Marietta, OH, U.S.A.) set at 26 °C with 75% humidity on a 12:12 h photoreversed light:dark cycle. To avoid any effect of previous mating experience on behaviour, we removed males from the large laboratory stocks prior to their final moult. Therefore, sexually mature males could not mate with females, ensuring that we only tested virgin males. Males were housed in 15-litre containers with about 30 males per container. Inside each 15-litre container crickets had access to egg cartons for shelter and access to water and Fluker's cricket food ad libitum. We monitored these boxes daily, then separated each male into an individual, 118 ml cup with a unique identifier upon eclosion. Throughout rearing, males were exposed to calling song produced by conspecifics reared in the same chamber. To avoid age-related variation in behaviour, we tested males 8—12 days posteclosion.

Song Models

The calling song of *T. oceanicus* males contains two important components in female choice: a trill-like long chirp consisting of six to nine pulses, followed by a series of paired, lower-amplitude pulses called short chirps (Fig. 1; Bailey & Zuk, 2009). Following Simmons et al. (2001), we constructed song models of varying proportions of long chirps to short chirps using the software package Raven v.1.2 (Cornell Lab of Ornithology, Ithaca, NY, U.S.A.). To maintain the song pulse lengths and the carrier frequency, we excised individual long- and short-chirp pulses from an Oahu calling song recorded in the wild at 23 °C. We then used the excised pulses to construct four song models that contained 20%, 40%, 60% and 80% long chirp, while holding other song parameters constant (see Bailey, 2008, for details). Our song models were comparable to average parameters measured in other Hawaiian *T. oceanicus* populations (Zuk, Rotenberry, & Simmons, 2001).

Phonotaxis Trials

We assessed male preference by conducting one phonotaxis trial per virgin male in an anechoic chamber at 23—26 °C under red light. We performed 153 phonotaxis trials in an arena measuring 155 cm long by 34 cm wide and 31 cm deep. On each of the long ends of the arena a speaker behind wire mesh played one of the four song models described above. Males were tested only once to mitigate the effects of prior acoustic experience on phonotaxis behaviour that can arise when individuals are repeatedly tested (Wagner, Smeds, & Wiegmann, 2001). For each trial, we randomly and independently assigned each male one of the four song models. We also randomized the direction of playback for each trial. To approximate the intensity of calling song that males typically experience in the wild, we maintained the playback intensity at 60 dB from the release point.

At the beginning of each trial, we positioned a single male 100 cm from the playback speaker and placed a plastic container 11 cm in diameter over him. Following a 2 min silent acclimation period, we began playback of one of the four song models. After 30 s of playback we lifted the container and allowed the cricket to freely roam inside the phonotaxis arena. Immediately after releasing a male, we began a 5 min observation period following the established protocol of Bailey and Zuk (2008). We chose a 5 min recording period because observations from the field suggest that if crickets do not begin moving within that period, they are unlikely to move or engage in satellite behaviour thereafter (M. Zuk, personal observations). Males were undisturbed throughout this 5 min observation period, during which we measured the following three characteristics of male responsiveness: (1) whether a male moved towards and settled near the playback speaker (within 5 cm of the playback speaker = positive response) or moved away from the playback speaker and settled on the side of the arena opposite the playback speaker (negative response); (2) if the response was positive, then we measured the latency to settle near the playback speaker; (3) the number of times that a male changed directions inside the testing arena, as a way to assess the strength of his phonotaxis to the playback speaker. We used latency to respond to the playback speaker as a proxy for the strength of an individual's phonotaxis behaviour and preference, as in other studies (Arbuthnott, Fedina, Pletcher, & Promislow, 2017; Bailey & Zuk, 2008; Gordon & Uetz, 2012; Pollack, 2003). Throughout the study, one person observed cricket behaviour and one person transcribed the data.

Analyses

We examined how wing morph affected all three measures of male responsiveness by performing three generalized linear models (GLM) using a maximum likelihood estimation method.

We began by examining how response type (positive versus negative: moving towards and settling near the playback speaker versus moving and settling away from the playback speaker) compared between flatwing males and normal-wing males. We used a GLM with response type as the dependent variable and wing morph and song model as fixed effects (N = 154). We also included an interaction term of wing morph by song model. Because the dependent variable had two equally likely outcomes (positive or negative response to the playback speaker), we used a GLM with a binomial distribution and a logit link function.

To compare the effect of song model and wing morph on the latency to respond to the playback speaker, we used a GLM with response time as the dependent variable and wing morph and song model as fixed effects (N = 114). We also included an interaction term of wing morph by song model. Because the data were not normally distributed (Shapiro−Wilk goodness-of-fit test: P = 0.0001), we log transformed the latency to respond, which normalized the data (Shapiro−Wilk goodness-of-fit test: P = 0.43; see Appendix, Figs A1, A2).

In our last model we examined how wing morph and response type affected the number of direction changes that males made before settling either on the same side or on the opposite side of the playback speaker (N = 141). We used a GLM with number of direction changes as the dependent variable and wing morph and response type as fixed effects. We also included an interaction term of wing morph by response type. Because our data was heavily weighted towards smaller values for the number of direction changes (Appendix, Fig. A3), we performed a GLM with a Poisson distribution and an identity link function.

Because our three measures of male responsiveness were not affected by pronotum length (i.e. body size; ANOVA: P = 0.94) or the side of the arena broadcasting calling song during a single trial (ANOVA: P = 0.82), we did not include these as covariates in our models. To ensure normality, we used a natural log transformation of response time and number of direction changes for all analyses.

We performed all analyses in JMP v.12.2 (SAS Institute Inc., Cary, NC, U.S.A.) using a significance level of 0.05.

Ethical Note

Our research adhered to ASAB/ABS guidelines for the use of animals in research and the legal requirements under the Animal Welfare Act of the United States Department of Agriculture-Animal and Plant Health Inspection Service (USDA-APHIS permit no. P526P-17-03395 to M. Zuk). We collected eggs from gravid females in research sites throughout Hawaii with permission from USDA-APHIS (permit no. P526P-17-03395 to M. Zuk). Laboratory colonies are maintained following all protocol set by USDA-APHIS. Animals were hand-collected without the use of animal traps with permission from USDA-APHIS. Laboratory colonies were maintained under conditions that simulated the field environment as closely as possible in temperature- and humidity-controlled incubators. Animals in laboratory incubators were checked daily and given water and food ad libitum. Animals are housed in 15-litre containers with about 30 males per container during rearing. We separated individuals upon eclosion to the penultimate instar, where they were individually housed for up to 12 days post-eclosion. Each individual was tested once at 8−12 days posteclosion and was never reused in the study. At the end of each day, males that were used in phonotaxis trials were euthanized by freezing for at least 24 h. Males were then autoclaved and disposed of in a biological waste container.

RESULTS

We found no overall effect of wing morph ($\chi^2_{1,154}$ = 0.012, P = 0.91) or song model on response type ($\chi^2_{3,154}$ = 0.78, P = 0.86). In about 70% of the trials, flatwing and normal-wing males responded positively by moving towards the play-back speaker (Fig. 2a). We also found a significant interaction of song model and wing morph on response type such that flatwing males responded negatively to the 40% long chirp song model more often than did normal-wing males ($\chi^2_{3,154}$ = 6.62, P = 0.01; Appendix, Table A1). However, overall we found no significant effect of the interaction between song model and wing morph on response type ($\chi^2_{3,154}$ = 7.03, P = 0.07).

With regard to response time, we found a significant effect of wing morph such that flatwings responded faster than normal wings to all song models ($\chi^2_{1,114}$ = 4.84, P = 0.03). Flatwings responded an average of 34 s faster than normal wings to all song models (Fig. 2b).

We found a significant effect of song model on response time, with the 60% long chirp song model eliciting a significantly faster response ($\chi^2_{3,114}$ = 6.32, P = 0.01) compared to the reference song model (Fig. 3, Appendix, Table A2). We also found a significant wing morph by song model interaction ($\chi^2_{3,114}$ = 4.76, P = 0.03), indicating that flatwings, but not normal wings, responded significantly faster to the 60% long chirp song model (Fig. 3, Appendix, Table A2). Overall, flatwings responded to the 60% long chirp model 31.6 s faster than they did to the 20% long chirp model, 46.9 s faster than they did to the 40% long chirp model and 74.5 s faster than they did to the 80% long chirp song model (Fig. 3).

Lastly, the number of direction changes was affected by both response type ($\chi^2_{1,141}$ = 51.88, P < 0.0001) and wing morph ($\chi^2_{1,141}$ = 9.46, P = 0.0021). However, we found no effect of the interaction between wing morph and response type on the number of direction changes ($\chi^2_{1,141}$ = 1.94, P = 0.16). Overall, males that responded negatively by moving and settling away from the playback speaker also changed direction in the testing arena significantly more compared with males that responded positively by moving towards and eventually settling near the playback speaker (Fig. 4, Appendix, Table A3). In general, flatwings moved around the testing arena less than normal wings, regardless of response type (Fig. 4, Appendix, Table A3).
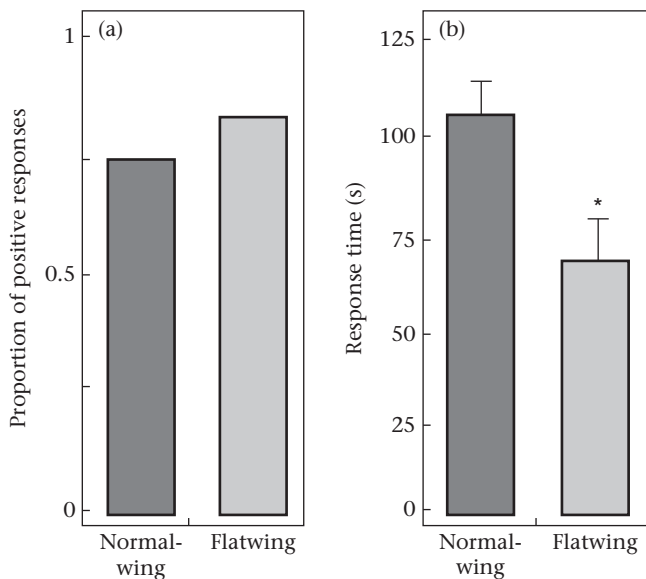

Figure 2. (a) Proportion of males positively responding by moving towards and settling near the playback speaker (N = 154). (b) Latency of males to positively respond to the playback speaker (N = 114). Error bars represent 1 SE. We tested each male once. During a 5 min observation period, we recorded whether a male responded positively to the playback speaker and, if so, how long it took to settle near the playback speaker. *P = 0.03.
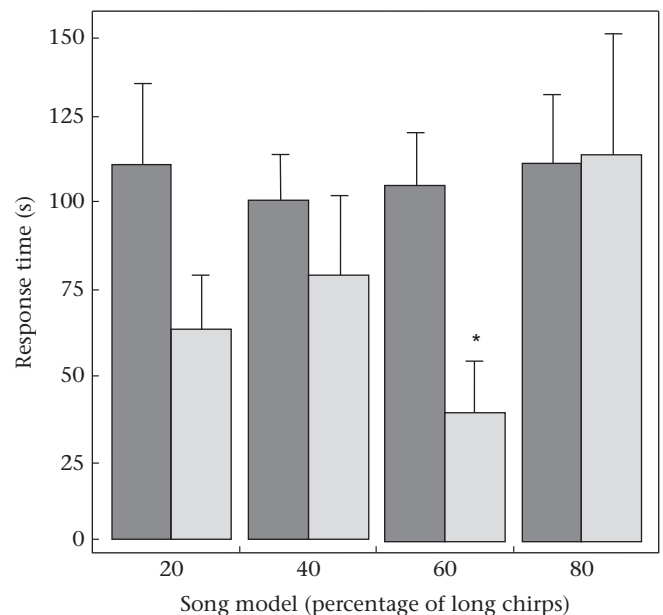

Figure 3. Latency of males to settle near the playback speaker broadcasting each of the song models (N = 114). Normal wings are represented in dark grey; flatwings are in light grey. Error bars represent 1 SE. We tested each male once and measured whether or not he responded positively by moving towards and settling near the playback speaker. If a male responded positively, we also measured his response time as the latency to settle near the playback speaker. *P = 0.03 (song model × wing morph on response time).
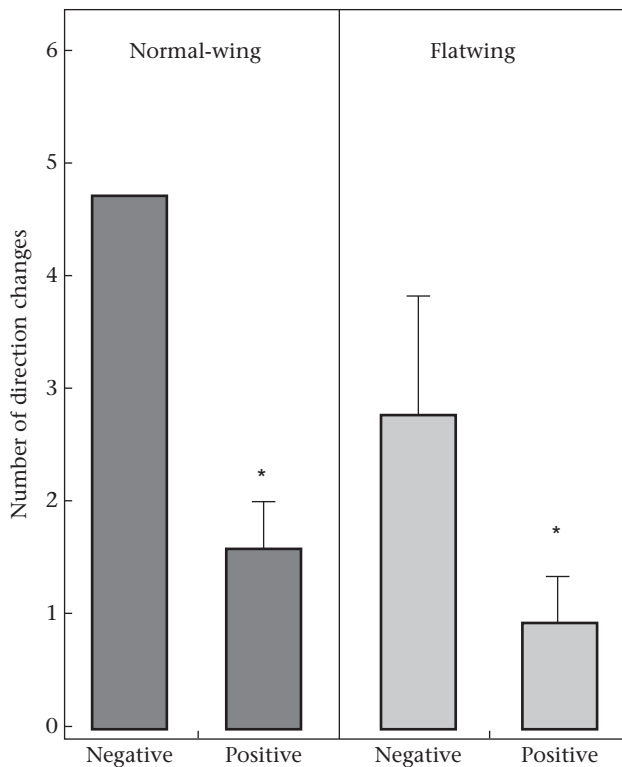
Figure 4. Number of direction changes when a male responded either positively by moving towards and settling near the playback speaker, or negatively by moving and settling away from the playback speaker ($N = 141$). Error bars represent 1 SE. We tested each male once. During a 5 min observation period, we measured the number of times a male changed direction in the testing arena relative to the playback speaker. *$P < 0.01$.

DISCUSSION

Several researchers have suggested that behavioural changes within the lifetime of an individual can shift selection such that additive genetic variance is exposed, allowing novel traits to evolve (Duckworth, 2009; Hunt, 2012). Zuk, Bastiaans, Langkilde, and Swanger (2014) argued that more flexible or plastic behaviours should have the greatest influence on the evolution of new traits. While it is likely that behavioural plasticity in response to the acoustic environment initially allowed the flatwing mutation to become established in Hawaii (Tinghitella, Wang, & Zuk, 2009), this does not necessarily explain how the flatwing mutation is maintained. Our results suggest that differences in reproductive behaviour may have been the result of subsequent selection on flatwings, despite the obvious disadvantages of obligate silence. Even though males with flatwings and those with normal wings positively responded to the playback speaker about the same amount, the flatwings responded fastest to the 60% long chirp song model, just like females. This suggests that flatwings are not simply engaging in satellite behaviour more than normal-wing males, but instead are adopting a specialized satellite strategy, in which they preferentially target attractive male signals. In preferentially targeting attractive male signals, flatwings have the potential to encounter more females and increase their reproductive success beyond that of facultative satellites.

Broadly, our work shows that males are discriminating among different signal qualities. Because males did not change direction very much inside the testing arena when exhibiting a positive response, this suggests that males are following certain decision rules with regard to their satellite strategy. In the wild, males that

hear a song that they do not prefer will likely move about until they detect an attractive call, after which they are likely to settle nearby and attempt to intercept approaching females. This is similar to what we are seeing in the testing arena, where males that are responding positively move towards and settle near the playback speaker. However, males that respond negatively will change directions and move around more before settling as far away from the playback speaker as is possible in the testing arena. While we know that males will sometimes associate with other males that females deem particularly attractive, especially in chorusing and lekking species (Beehler & Foster, 1988; Pfennig, Rapa, & McNatt, 2000), our study is the first to demonstrate this phenomenon in a system with an obligate satellite strategy, where adopting a 'good' satellite strategy (i.e. one that increases the chances of encountering females) is especially important because males have no other means of attracting mates.

Such discrimination raises a larger question about how male attendance to male signals affects the evolution of secondary sexual characteristics. Much research shows that female preference for male signals can drive the evolution of elaborate male traits (reviewed in Rosenthal, 2017), little parallel research has examined the evolutionary causes and consequences of male attendance to male sexual signals, although we have some evidence that males may assess their opponents in agonistic contests (Painting & Holwell, 2014; Stuart-Fox, 2006). Here we arrive at a paradoxical conclusion in which males with exceptionally attractive songs do not always have the highest mating success. Even though females prefer calling songs with 60% long chirp, males producing such songs are also more likely to attract satellite males. Therefore, male preference for male signals may actually oppose selection by females on male sexual traits, potentially slowing the rate of male trait evolution. At the same time, this could increase competition between calling and satellite males, further driving selection on mate attraction. Our work suggests an area of future research on sexual selection via male−male preference.

The ability to discriminate among signalling males may be a window into how satellite behaviour is maintained. Much research has been devoted to the question of how discontinuous variation in male mating behaviour is maintained (reviewed in Oliveira, Taborsky, & Brockmann, 2008), and while many suggest that alternative strategies are 'making the best of a bad job' (West-Eberhard, 2003), this need not be the case. Previous work has shown that satellite behaviour can be as successful as calling in some cricket populations (Rowell & Cade, 1993; Walker & Cade, 2003). Here we show that by discriminating among callers, satellite males may gain greater access to females while also escaping the costs associated with signalling. This may provide equal or even greater fitness to satellites. Because of the potential for equal fitness benefits and functional equivalence, many have concluded that like evolutionarily stable strategies, alternative tactics are maintained by frequency-dependent selection particularly with regard to conditional versus mixed strategies (Plaistow et al., 2004). Further work will explore the role of frequency dependence in satellite behaviour and the success of flatwing.

Author Contributions

R.M.O. and M.Z. designed the experiment; R.M.O. collected the data, carried out data analysis and prepared the manuscript; M.Z. critically reviewed the manuscript.

Competing Interests

We do not have any competing interests in this research.

Data Availability

Acknowledgments

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Appendix

Table A1
Summary table of generalized linear model with response type (positive versus negative) as the dependent variable and wing morph, song model, and an interaction of wing morph by song model as the fixed effects ($N = 154$)

Term	Estimate	SE	χ^2	P
Intercept	−1.26	0.27	27.22	**<0.0001**
Wing morph [FW]	−1.23	0.27	0.012	0.91
Song model (20% long chirp)	−1.65	0.49	0.72	0.4
Song model (40% long chirp)	−1.17	0.45	0.039	0.84
Song model (60% long chirp)	−1.06	0.42	0.22	0.64
Wing morph [FW]∗song model (20% long chirp)	−1.83	0.49	1.6	0.21
Wing morph [FW]∗song model (40% long chirp)	0.12	0.45	6.62	**0.01**
Wing morph [FW]∗song model (60% long chirp)	−1.18	0.42	0.03	0.86

FW: flatwing. Significant outcomes ($P < 0.05$) are shown in bold.

Table A2
Summary table of generalized linear model with response time as the dependent variable and wing morph, song model, and an interaction of wing morph by song model as the fixed effects ($N = 114$)

Term	Estimate	SE	χ^2	P
Intercept	4.31	0.075	386.09	**<0.0001**
Wing morph [FW]	4.14	0.075	4.84	**0.03**
Song model (20% long chirp)	4.32	0.11	0.022	0.88
Song model (40% long chirp)	4.38	0.15	0.28	0.62
Song model (60% long chirp)	3.98	0.13	6.32	**0.01**
Wing morph [FW]∗song model (20% long chirp)	4.25	0.11	0.21	0.65
Wing morph [FW]∗song model (40% long chirp)	4.44	0.15	0.85	0.35
Wing morph [FW]∗song model (60% long chirp)	4.02	0.13	4.76	**0.03**

FW: flatwing. Significant outcomes ($P < 0.05$) are shown in bold.

Table A3
Summary table of generalized linear model with the number of direction changes towards and away from the playback speaker as the dependent variable and wing morph, response type (positive versus negative), and an interaction of wing morph by response type as the fixed effects ($N = 141$)

Term	Estimate	SE	χ^2	P
Intercept	2.53	0.2	160.36	**<0.0001**
Wing morph [FW]	1.84	0.2	9.46	**0.0021**
Response [Neg]	3.69	0.2	51.88	**<0.0001**
Response [Neg]∗wing morph [FW]	2.24	0.2	1.94	0.16

FW: flatwing. Significant outcomes ($P < 0.05$) are shown in bold.

Figure A2. Q–Q plot for log-transformed response time. Data became more normally distributed (i.e. form a graph with a bell-shaped curve) after log transformation. Furthermore, a Shapiro–Wilk goodness-of-fit test yielded a P value of 0.43, indicating a normal distribution following a log transformation.
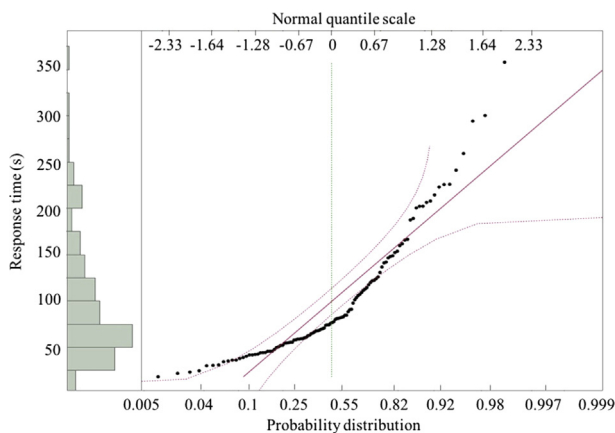

Figure A1. Q–Q plot for response time, prior to log transformation. Data were heavily skewed towards longer response times. A Shapiro–Wilk goodness-of-fit test yielded a P value of 0.0001, indicating that the data were not normally distributed.
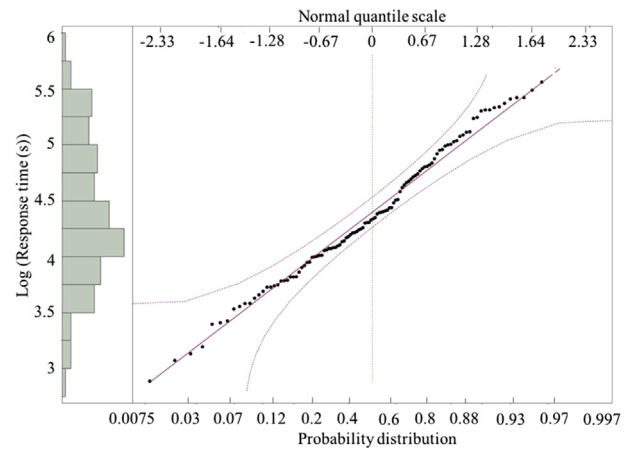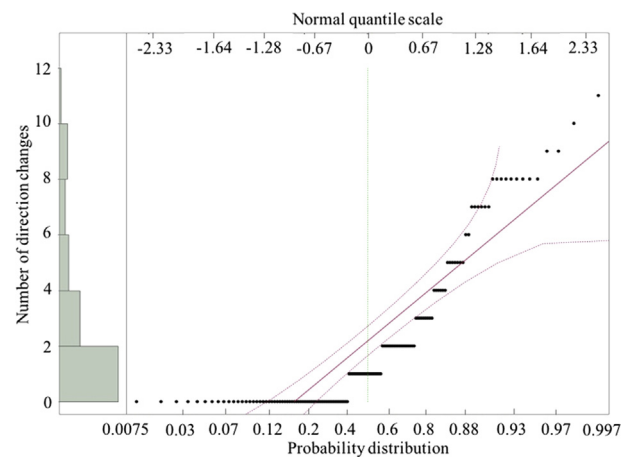

Figure A3. Q–Q plot for the number of direction changes prior to log transformation. The data were heavily skewed towards smaller numbers. A Shapiro–Wilk goodness-of-fit test yielded a P value of 0.0001, indicating that the data were not normally distributed.