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Limited flexibility in female Pacific field cricket (*Teleogryllus oceanicus*) exploratory behaviors in response to perceived social environment

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Abstract

How populations adapt, or not, to rapid evolution of sexual signals has important implications for population viability, but is difficult to assess due to the paucity of examples of sexual signals evolving in real time. In Hawaiian populations of the Pacific field cricket (*Teleogryllus oceanicus*), selection from a deadly parasitoid fly has driven the rapid loss of a male acoustic signal, calling song, that females use to locate and evaluate potential mates. In this newly quiet environment where many males are obligately silent, how do phonotactic females find mates? Previous work has shown that the acoustic rearing environment (presence or absence of male calling song) during late juvenile stages and early adulthood exposes adaptive flexibility in locomotor behaviors of males, as well as mating behaviors in both sexes that helps facilitate the spread of silent (flatwing) males. Here, we tested whether females also show acoustically induced plasticity in walking behaviors using laboratory-reared populations of *T. oceanicus* from Kauai (HI; >90% flatwings), Oahu (HI; ~50% flatwings), and Mangaia (Cook Islands; no flatwings or parasitoid fly). Though we predicted that females reared without song exposure would increase walking behaviors to facilitate mate localization when song is rare, we discovered that, unlike males, female *T. oceanicus* showed relatively little plasticity in exploratory behaviors in response to an acoustic rearing environment. Across all three populations, exposure to male calling song during development did not affect latency to begin walking, distance walked, or general activity of female crickets. However, females reared in the absence of song walked slower and showed a marginally non-significant tendency to walk for longer durations of time in a novel environment than those reared in the presence of song. Overall, plasticity in female walking behaviors appears unlikely to have facilitated sexual signal loss in this species.

KEYWORDS
behavioral plasticity, exploration, locomotor behavior, mate localization, Pacific field cricket, sexual signal loss

1 | INTRODUCTION

Sexual signals often reflect a balance between natural and sexual selection—while sexual selection tends to favor trait elaboration, natural selection often provides a braking force that favors trait reduction (Heinen-Kay et al., 2015; Zuk & Kolluru, 1998). In some cases, the delicate balance between these selective forces can tip, and natural selection can drive the evolutionary loss of a sexual signal (Wiens, 2001; Zuk, Rotenberry, & Tinghitella, 2006). Sexual signals are critical for successful reproduction and maintenance of species boundaries because they are often required for mate localization and attraction. Thus, rapid changes in sexual traits can pose major implications for the signaler, receiver, and population viability (Mendelson, Martin, & Flaxman, 2014; Panhuis, Butlin, Zuk, & Tregenza, 2001; Safran, Scordato, Symes, Rodriguez, & Mendelson, 2013). Understanding how populations adapt, or not, to such a dramatic shift in the mating system is of critical importance, but remains difficult to study because so few contemporary examples of rapid sexual signal evolution are known (Svensson & Gosden, 2007).

Pacific field crickets (*Teleogryllus oceanicus*) offer a rare opportunity to investigate how populations cope with rapid evolutionary loss of an acoustic sexual signal. These crickets are native to Australia and the South Pacific, and have been introduced to Hawaii (Otte, 1994; Otte & Alexander, 1983). Males produce a long-range acoustic signal, calling song, that females use to locate and evaluate potential mates (Simmons, Zuk, & Rotenberry, 2001). Only in Hawaii, *T. oceanicus* co-occurs with a deadly parasitoid fly, *Ormia ochracea*, that exploits male song to locate its cricket host. Selection from the fly has driven a suite of adaptive shifts in cricket song and behaviors (Cade, 1975; Rotenberry, Zuk, Simmons, & Hayes, 1996; Zuk, Simmons, & Cupp, 1993). Recently, a novel mutation arose and rapidly spread (<20 generations) on the Hawaiian island of Kauai that produced a silent male morph, "flatwing" (Pascoal et al., 2014; Zuk et al., 2006). A few years later, an independent mutation that yields a similar phenotype became established on Oahu (Pascoal et al., 2014). Today, ~90% of males on Kauai and ~50% of males on Oahu are flatwing (Pascoal et al., 2014; Zuk, Bailey, Gray, & Rotenberry, 2018). Because flatwing males lack the wing structures necessary to produce song, they are protected from parasitism by the fly, but are unable to call to attract females. One major consequence of the rapid spread of flatwing males is that some Hawaiian populations are now nearly devoid of conspecific song.

This acoustic sexual signal loss presents two important implications for females. First, acoustic signals are used for mate localization as well as evaluation, so the loss of song requires novel mate searching strategies. Female *T. oceanicus* are highly phonotactic and use male calling song to localize mates, so it is unclear how females find mates in the newly song-scarce environment. Second, acoustic signal loss alters the perceived social environment by producing cues that would historically indicate that males are scarce, either due to low population density or female-biased sex ratio. This indirect genetic effect of acoustic signal loss—a change in the social environment caused by trait evolution (Moore, Brodie, & Wolf, 1997; Wolf, Brodie, Cheverud, Moore, & Wade, 1998)—has been well documented in its ability to expose adaptive plasticity in mating behaviors, and it appears to play a key role in accommodating novel traits (Bailey, Gray, & Zuk, 2010; Bailey & Zuk, 2008; Kasumovic, Hall, & Brooks, 2012; Zuk, Bastiaans, Langkilde, & Swanger, 2014; Zuk & Tinghitella, 2008). When reared without exposure to calling song, *T. oceanicus* of both sexes are more phonotactic and females are less choosey about male song quality than counterparts reared in a song-rich environment (Bailey & Zuk, 2008, 2012; Bailey et al., 2010). This behavioral plasticity, in combination with generally more permissive mating behaviors in the Hawaiian Islands, particularly Kauai, likely helped the population persist during early stages of flatwing establishment (Tinghitella & Zuk, 2009).

The acoustic rearing environment has recently been shown to influence male locomotor behaviors (Balenger & Zuk, 2015). When reared without song exposure, male *T. oceanicus* from Kauai (though not other populations) exhibit greater exploratory behaviors (i.e., spend more time walking, walk sooner after being placed in a novel environment, and are generally more active) than counterparts raised in a song-rich environment (Balenger & Zuk, 2015). Exploratory behaviors are important in the context of mate searching, though they are also relevant for foraging and predator avoidance (Reale, Reader, Sol, McDougall, & Dingemanse, 2007). The upshift in walking behaviors is believed to help males adopt an alternative mating strategy where males act as satellites to the few remaining callers and intercept females responding to their song (Bailey et al., 2010; Balenger & Zuk, 2015; Zuk et al., 2006). In crickets, females typically conduct the mate searching by responding to calling song of stationary males, though walking around also appears important in acquiring mates (Hissmann, 1990). Prior to the spread of flatwing, a song-less acoustic environment could have occurred following a catastrophic event, such as a large storm, that reduced the population density. In such an event, females may have been more likely to encounter a male by modifying behaviors that allow them to more effectively sample their environment, such as walking for longer durations of time or greater distances than they would if perceiving cues that males are abundant. We thus hypothesized that females should also show plasticity in locomotor behaviors in response to the perceived social environment.

In this study, we examined how exposure to calling song during late juvenile and early adult rearing affects exploratory behavior in female *T. oceanicus*. We predicted that female crickets reared in a song-less environment would show greater locomotor behaviors (e.g., walk greater distances, spend more time walking, walk faster), as this may improve the probability of encountering a mate. We focused on three populations that differ in evolutionary history with the parasitoid fly and proportion of flatwing males: Kauai, HI, USA (fly present; ~90% flatwings), Oahu, HI, USA (fly present; ~50% flatwings), and Mangaia, Cook Islands (fly absent; no flatwings) (Pascoal et al., 2014; Zuk et al., 1993, 2018). This comparative

approach allowed us to disentangle whether potential differences between acoustic treatments are due to selection subsequent to the establishment of flatwing (i.e., if plasticity is only evident in Kauai), or reflect a pre-existing, species-level response (i.e., if responses are similar across populations).

2 | METHODS

2.1 | Experimental animals

The laboratory colony of *T. oceanicus* from Kauai was established in 2003 after the discovery of the flatwing morph. The Oahu colony was established in 1993 and the Mangaia colony was established in 2009. Hawaiian laboratory colonies have been supplemented with wild eggs at least annually to maintain genetic variation and represent wild populations. Juvenile crickets were reared in 15-L plastic containers with egg carton for shelter and ad lib access to food (Teklad high fiber rabbit chow) and water. Cricket colonies were housed within Caron Insect Growth Chambers (model 6025) set at 26°C, 75% humidity, and a 12:12 photo-reversed L:D cycle. At least 2 weeks prior to adult eclosion, juvenile female crickets were isolated in 118-ml plastic containers with egg carton for shelter and ad lib access to food and water, and randomly assigned to either "Song" or "No Song" acoustic treatment. Females were checked daily for adult eclosion.

2.2 | Acoustic rearing treatments

The "Song" and "No Song" experimental incubators were both lined with sound-absorbing foam, including internal walls and shelves, and equipped with six Sony SRS-M30 speakers and three Sony CD players. Only in the "Song" incubator, average calling song from the focal population was broadcast at 80–85 dB-SPL measured at lid of rearing container with an AZ sound meter model 8922 (Bailey et al., 2010). Calling song was played during the crickets' active cycle (9:00–21:00) during the dark photoperiod. Acoustic treatments, and the crickets assigned to a given treatment, were periodically swapped between incubators. Crickets were placed in the "No Song" incubator at least 16 hr prior to behavioral trials to ensure that observed behaviors reflect rearing treatment and not a short-term change in acoustic environment. Crickets are highly responsive to the songs of their own species, and it is unlikely that any observed behavioral differences would occur in response to differences in exposure to sound rather than conspecific song. Furthermore, crickets reared in the "No Song" incubator were not raised in complete silence, but rather in the absence of conspecific calling song.

2.3 | Behavioral trials

Trials were conducted with virgin female *T. oceanicus* 8–12 days after adult eclosion. Trials took place during the crickets' normal active hours inside a 22.0–24.2°C anechoic room under red light. The experimental arena was a 149 × 149 cm square with 31-cm high walls, and had a 6 × 6 grid drawn on the craft paper floor. Accordion-folded wire mesh covered the bottom of the arena to provide the crickets with cover while allowing the observer to see the crickets' movements.

The focal female was allowed to acclimate for 3 min under a 118-ml cup on a small piece of craft paper in the center of the arena. A new piece of craft paper was used for each female to minimize the accumulation of chemical cues. After the acclimation period, the cup was lifted, allowing the cricket to freely roam the novel arena for the silent, 7-min trial. We recorded latency to first movement (directional movement of at least one body length), total time spent walking (s), number of unique squares entered (at least half body length), and number of gridlines crossed (at least half body length). The number of unique squares entered provides a metric of distance by indicating how much of the arena the cricket walked in. In addition to serving as a secondary metric of distance, the number of gridlines crossed provides an indication of general activity as it is possible for a cricket to cross many gridlines while not covering much of the arena (i.e., by walking back and forth across the same gridline). To assess walking speed, we calculated the number of gridlines crossed per total time walking and the number of unique squares entered per total time walking (i.e., distance/time). Observers (DBS and JHK) were treatment blind for most trials, though this did not influence results (see below).

2.4 | Data analysis

Data were analyzed in JMP Pro version 13.0. A generalized linear model with binomial distribution revealed that crickets that failed to move during the 7-min trial did not differ from those that did move in association with population (χ_2^2 = 3.060, p = 0.217) or rearing treatment (χ_1^2 = 0.627, p = 0.429), so they were excluded from subsequent analyses. After removing non-movers (24 individuals), we were left with the following sample sizes: Mangaia (No Song = 48, Song = 47), Oahu (No Song = 56, Song = 62), and Kauai (No Song = 44, Song = 39).

We used separate general linear models to analyze the following response variables: latency to move (s), total time walking (s), number of gridlines crossed, number of unique squares entered, gridlines crossed/total time walking, and unique squares entered/total time walking. To improve normality, we log-transformed latency to move and unique squares entered/total time walking, and square-root transformed number of gridlines crossed. All other responses were normally distributed. For each response, we ran a full model containing the following predictors: acoustic treatment, population, acoustic treatment*population, age (days past adult eclosion), treatment blind, and observer. The interaction term and latter three variables were excluded from final analyses due to non-significance, except for the two speed metrics which showed a significant observer effect in the case of gridlines/time, and nearly significant observer effect for unique squares/time. Thus, most final analyses included just population and acoustic treatment as predictors; gridlines crossed/total time walking and log-transformed unique squares entered/total time additionally included observer.

TABLE 1   Results of separate general linear models examining female *Teleogryllus oceanicus* exploratory behaviors

Response	Predictor	F	df	p	FDR-adjusted p
Latency to move (s) (Log transformed)	Acoustic treatment	0.120	1, 292	0.730	0.786
	Population	1.794	2, 292	0.168	0.251
Total time walking (s)	Acoustic treatment	4.405	1, 292	**0.037**	*0.073*
	Population	3.640	2, 292	**0.028**	*0.064*
# Gridlines crossed (Square root transformed)	Acoustic treatment	0.172	1, 292	0.678	0.786
	Population	0.172	2, 292	0.680	0.786
# Unique squares entered	Acoustic treatment	0.025	1, 292	0.874	0.874
	Population	4.154	2, 292	**0.017**	**0.047**
Gridlines crossed/total time walking (s)	Acoustic treatment	3.712	1, 291	*0.055*	0.096
	Population	1.729	2, 291	0.179	0.251
	Observer	7.704	1, 291	**0.006**	**0.041**
Unique squares entered/total time walking (s) (Log transformed)	Acoustic treatment	9.010	1, 291	**0.003**	**0.041**
	Population	4.358	2, 291	**0.014**	**0.047**
	Observer	6.676	1, 291	**0.010**	**0.047**

Significant *p*-values (*p* < 0.05) are bolded, and marginally non-significant *p*-values (*p* < 0.08) are italicized.

In an attempt to understand the nature of observer effects on speed, we conducted additional general linear models for gridlines crossed/total time walking and log-transformed unique squares entered/total time walking that included the following predictors: population, acoustic treatment, observer, observer*population, and observer*acoustic treatment. In these analyses, the interaction terms are primarily of interest—if the observer does not interact with either acoustic treatment or population, then any significant observer effects do not affect the interpretation of results from the main analyses.

In cases of significant population effects, we used Tukey HSD to disentangle group differences. Conducting multiple tests on data from the same trials can increase the Type 1 error rate, so we controlled for this using the False Discovery Rate (FDR; Benjamini & Hochberg, 1995) add-in for JMP.

3 | RESULTS

Latency to move did not differ between populations or acoustic rearing treatments (Table 1, Figure 1a). After adjusting for FDR, females reared in the absence of conspecific calling song displayed a marginally non-significant trend toward spending more time walking than counterparts reared in the presence of song (Table 1, Figure 1b). Populations also showed marginally non-significant differences after adjusting for FDR in total time spent walking (Table 1, Figure 1b), where Mangaia crickets tended to walk for longer durations of time than crickets from Kauai (*p* = 0.026); Oahu females were not different from either Kauai (*p* = 0.106) or Mangaia (*p* = 0.750). The number of unique squares entered differed between populations, but not acoustic rearing treatments (Table 1, Figure 1c). Tukey HSD revealed that crickets from Mangaia entered more unique squares, and hence walked a greater distance than those from the Hawaiian populations

of Oahu (*p* = 0.025) and Kauai (*p* = 0.050). The number of gridlines crossed did not differ between populations or acoustic treatments (Table 1, Figure 1d). After controlling for FDR, the number of unique squares entered/time spent walking differed significantly between acoustic treatments and populations (Table 1, Figure 1e). "No Song" females walked slower, entering fewer unique squares per second than "Song" counterparts. Tukey HSD showed that Mangaia females walked faster than those from Oahu (*p* = 0.012), and Kauai crickets were not different from either Mangaia (*p* = 0.614) or Oahu (*p* = 0.163). Gridlines crossed/time spent walking showed non-significant effects of populations or acoustic rearing treatments, though it trended in the same direction as #squares entered/time spent walking for acoustic rearing treatment (Table 1, Figure 1f). Both metrics of speed showed significant observer effects (Table 1). Secondary analyses did not reveal significant interactions between observer and acoustic treatment (gridlines/time: $F_{1,288}$ = 0.033, *p* = 0.856; unique squares/time: $F_{1,288}$ = 0.074, *p* = 0.786) or population (gridlines/time: $F_{2,288}$ = 0.514, *p* = 0.599; unique squares/time: $F_{2,288}$ = 0.280, *p* = 0.756). Thus, although observers differed for speed metrics, they were not biased in a way that affects the interpretation of results.

4 | DISCUSSION

The goal of our study was to test whether female *T. oceanicus* raised in an environment devoid of conspecific calling song, mimicking low population density or high proportion of silent flatwing males, increased exploratory walking behaviors. Both sexes have previously been shown to exhibit strong pre-existing plasticity in mating behaviors that helped pave the way to male sexual signal loss (e.g., Bailey & Zuk, 2008, 2012; Bailey et al., 2010). Additionally, males from the island of Kauai show plasticity in locomotor behaviors, walking greater
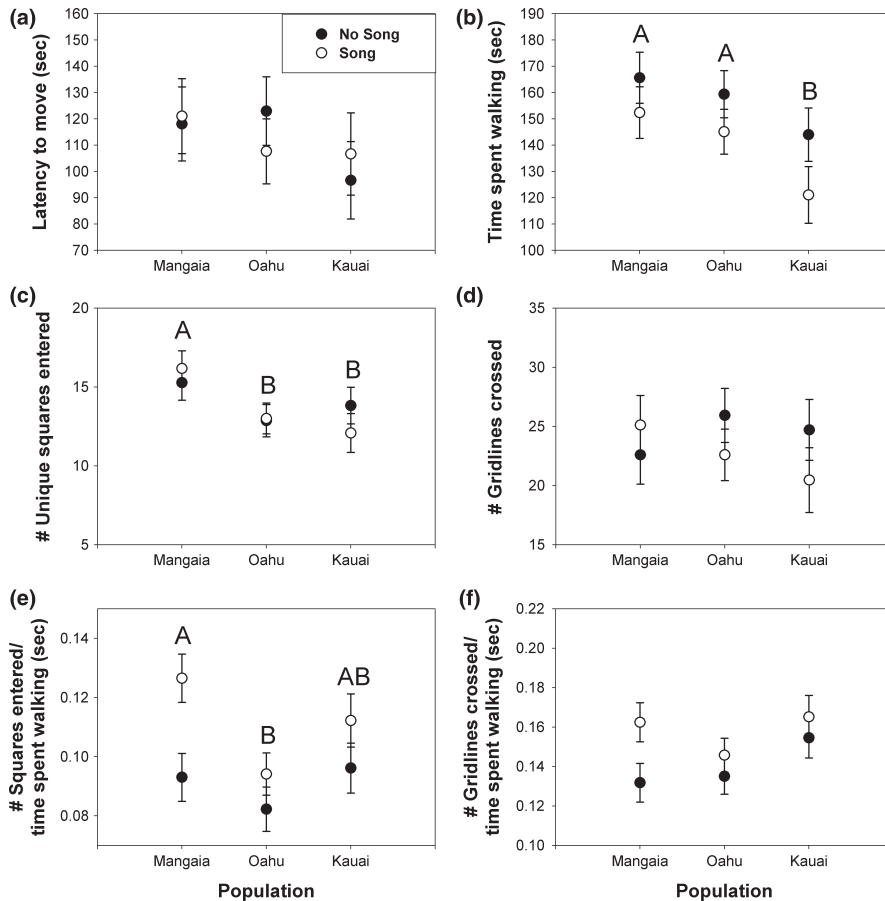
FIGURE 1 Female *Teleogryllus oceanicus* reared in the absence of song are indicated with closed circles; those reared in the presence of calling song have open circles. LS means ± *SE* are depicted. Letters denote population differences as determined by Tukey HSD. Legend in (a) applies to all panels. (a) Latency to begin walking did not differ between acoustic rearing treatments. (b) Females showed a marginally non-significant tendency to spend more time walking when reared without song exposure. Acoustic treatment did not affect (c) the number of unique squares entered or (d) the number of gridlines crossed. (e) Females reared in the absence of song entered fewer unique squares per second than those raised in the presence of song, though acoustic treatment did not influence (f) the number of gridlines crossed per second

distances for longer durations of time when raised in the absence of calling song (Balenger & Zuk, 2015). Given male flexibility in walking behaviors and the fact that females tend to do the mate searching in the species, we hypothesized that similar plasticity in female walking behaviors could have contributed to the rapid spread of silent flatwing morphs by providing an alternative mechanism for locating potential mates.

We did not discover support for our prediction—unlike Kauai males, female *T. oceanicus* from multiple populations showed little plasticity in walking behaviors. Acoustic rearing environment did not influence the overall distance moved, activity level, or latency to begin walking of female crickets. Only one of the six aspects of walking behavior we measured, walking speed, unequivocally differed between acoustic environments, but in the opposite direction that we predicted. Walking appears critical for female gryllids to encounter mates at both high and low population densities (Hissmann, 1990), so perhaps female *T. oceanicus* show relatively low levels of plasticity in locomotor behaviors because they already walk quite a bit regardless of social cues. It is also possible that the other ecological applications of locomotor behavior, such as foraging and predator avoidance, are more important contributors to the expression and evolution of female walking behaviors than mate searching.

When raised in the absence of song, female *T. oceanicus* from all three populations explored the novel arena significantly slower than those reared in the presence of song. Females reared without song exposure also showed a marginally non-significant (after adjusting for FDR) tendency to walk for longer durations of time. Perhaps walking slowly but consistently makes it more likely for females to hear males calling in the distance or pick up chemical cues (i.e., cuticular hydrocarbons) from other crickets on the ground. However, if this represented an adaptive strategy when males are rare or not calling, we would have expected this effect to be strongest in Kauai, which is not consistent with our results. Another possible explanation for plastic differences in speed is that walking faster is beneficial for females with prior experience of calling males. Female *G. integer* can recall the location of previously calling males, though it is unclear whether this involves cognitive function (i.e., memory) or retracing chemical cues laid during prior sampling (Wiegmann, 1999). Female *T. oceanicus* are able to remember information about attractiveness of previously encountered males during mating decisions (Bailey & Zuk, 2009). If female crickets can additionally remember the location of calling males, it is possible that females reared in a song-rich environment walk faster because prior experience indicates that males are close by. Further research is needed to understand whether differences in walking speed are advantageous in populations that differ in the proportion of flatwing males or population density.

Populations differed in some aspects of walking behavior. Females from Mangaia, where both the parasitoid fly and flatwing cricket morph do not exist, covered the greatest distance, walked the fastest, and showed a tendency to spend more time walking. Crickets from the two Hawaiian populations walked a shorter distance than those from Mangaia, which is the opposite direction predicted if increased walking helped locate mates in silent conditions. However, the Hawaiian populations did not differ consistently from Mangaia. Kauai was indistinguishable from Mangaia for speed, and Oahu did not differ from Mangaia for time spent walking. Thus, these population differences likely do not reflect an adaptive response to presence/absence of flatwing males and the parasitoid fly, or other possible ecological differences between populations. Rather, *T. oceanicus* populations show a clear pattern of genetic isolation by geographic distance, and island populations in particular show evidence of recent bottlenecks and relatively low allelic diversity (Pascoal et al., 2016; Tinghitella, Zuk, Beveridge, & Simmons, 2011). Thus, it is not surprising that populations may differ due to genetic drift rather than selection.

Flexibility in exploratory behaviors associated with acoustic environment differs between the sexes in a population-specific manner. Females from all three populations walked slower when raised without song, but otherwise showed surprisingly little socially derived plasticity in walking behaviors. However, males from Kauai—where the vast majority of males are flatwing—appear to have experienced selection subsequent to the spread of flatwing for flexibility in walking behaviors in response to the acoustic environment, while Oahu and Mangaia males showed little to no plasticity in locomotion (Balenger & Zuk, 2015). Increased walking behaviors exhibited by Kauai males reared in the absence of song are thought to improve the success of an alternative mating strategy, satellite behavior, that is particularly important for flatwings (Balenger & Zuk, 2015; Zuk et al., 2006). When acting as a satellite, males use phonotaxis to approach other calling males and attempt to intercept females responding to the male calls. While this shift toward greater reliance on satellite behavior, facilitated by flexible locomotor behaviors, is likely a critical factor underlying the spread and maintenance of silent flatwing morphs (Bailey et al., 2010; Zuk et al., 2006), our study shows that female locomotor behavior is largely inflexible in response to acoustic social cues, and is thus unlikely to have helped accommodate the evolutionary loss of male song.

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