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Phenotypic Plasticity, Behavioral Syndromes and Their Evolutionary Implications in  
Pacific Field Cricket Females

A Thesis submitted in partial satisfaction  
of the requirements for the degree of

Master of Science

in

Evolution, Ecology, and Organismal Biology

by

Nadya Dimitrova Dimitrova

June 2015

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2015

The Thesis of Nadya Dimitrova Dimitrova is approved:

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## ABSTRACT OF THE THESIS

### Phenotypic Plasticity, Behavioral Syndromes and Their Evolutionary Implications in Pacific Field Cricket Females

by

Nadya Dimitrova Dimitrova

Master of Science, Evolution, Ecology, and Organismal Biology  
University of California, Riverside, June 2015  
Dr. Marlene Zuk, Chairperson

Two models have been suggested to predict the presence of behavioral syndromes (correlations between different behaviors or the same behavior in different contexts). According to "genetic constraint" models, such correlations, where present, should persist regardless of environmental changes, while "adaptive divergence" models posit that syndromes will exist only where beneficial, and one such case is a high predation environment. We examined the plasticity and potential correlation between two behaviors - female responsiveness to male calls (responsiveness) and latency to emerge from shelter after a simulated predator threat (boldness). The subjects were female Pacific field crickets (*Teleogryllus oceanicus*) from populations with different predation pressures, and as an additional, experimental proxy for predation pressure, they were reared in an environment simulating either high or low population density. As expected,

females reared in incubators where low population density was simulated, were more responsive to male calls, since such environments signal less mating opportunities. However, regardless of rearing conditions, females from the population where parasitoid predation pressure was strongest, were more responsive to male calls and also less bold, which suggests that there are genetic differences between the populations as well. As predicted by divergence models, the only population in which a behavioral syndrome (bold/more responsive) was detected, suffered the highest rate of parasitoid larvae infestation. If predation has driven the formation of bold/more responsive and shy/less responsive coping styles in females in this population, such strategies could be adaptive due to a tradeoff mechanism. A boldness/responsiveness syndrome was also present in both the high and low population density environments, which could be explained by both genetic constraint and adaptive divergence models - different experiments, and in some instances larger sample sizes, are needed to clarify this result.

Keywords: behavioral syndromes, phenotypic plasticity, female choice, *Teleogryllus oceanicus*, predation pressure

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## Chapter 1

# Phenotypic plasticity, behavioral syndromes and their evolutionary implications in Pacific field cricket females

## INTRODUCTION

Stable behavioral traits in individuals, or personality types, were once only ascribed to humans, but it is now known that they exist across a broad range of animal taxa and are heritable (Dingemanse et al. 2002; Stirling et al. 2002; Bell 2007; Bergmüller and Taborsky 2010; Kortet and Hedrick 2012). Moreover, correlations between different behaviors (e.g. aggression and boldness), or the same behavior in different contexts, termed behavioral syndromes, have been observed in many species and various configurations (Sih et al. 2004; Hedrick and Kortet 2006; Bell 2007; Dingemanse et al. 2007; Wilson et al. 2010). Due to the effects of pleiotropy, physiology, and linked genes (Sih et al. 2004; Dingemanse and Reale 2005; Bell 2007) such correlations are not uncommon and can in some cases evolve rapidly, requiring little genetic change (West-Eberhard 1989).

Two types of models have been proposed for the stability of behavioral syndromes, and there has been some support for both. “Genetic constraint” models predict that correlations among behaviors are stable and should be the same within and between populations and in different environments, whereas according to “adaptive divergence” models they are a function of the environment and are expected to differ in different conditions (Dingemanse and Reale 2005). Considering behavioral syndromes can be useful when, for example, a behavior in a specific context is not optimal, because this may be the result of a correlation of that behavior with other more adaptive behaviors (Johnson and Sih 2007). Correlations can also affect the distribution of populations

(Fraser et al. 2001), their potential to be invasive (Sih et al. 2004), and even the parasites and diets of different individuals within a population (Wilson et al. 1993).

Since most behaviors (reactions to internal or external stimuli) are plastic (West-Eberhard 1989; Pfennig et al. 2010), we can't effectively study them or their correlations, without considering plasticity. The role of phenotypic plasticity in evolution is not one directional - it may slow down the rate of genetic change by making the same genotype more adaptable to different conditions, but it may also result in plastic traits, such as behavior, exhibiting greater genetic variation, because they offer a greater possibility for diversification within and between environments (Via and Lande 1985; West-Eberhard 1989; Pfennig et al. 2010). It is known that female choice can be plastic (Chaine and Lyon 2008) and some environmental factors that affect it in different species include diet (Hunt et al. 2005), rearing temperature (Rodriguez and Greenfield 2003), age (Wilson et al. 2010), predation risk (Hedrick and Dill 1993), and reproductive state (Lynch et al. 2005). In the context of behavioral syndromes, however, sexual selection has been poorly studied (Sih et al. 2004; Schuett et al. 2008; Sih et al. 2010) and even more so when it comes to variation in female choice (Jennions and Petrie 1997). There is some experimental evidence that female sexual responsiveness can be correlated with other behaviors (Wilson et al. 2010), but to our knowledge the relationships between plasticity, behavioral correlations, and their evolutionary implications, have not been considered in a sexual selection context. Here we examine the correlation between female responsiveness to male calls (responsiveness hereafter) and boldness (latency to emerge

from shelter after a simulated predator threat) in the Pacific field cricket, *Teleogryllus oceanicus*.

Our system is particularly well suited for such a study, because we were able to use individuals from the same population before and after the spread of a mutation which changed one of the selective forces (predation pressure by parasitoids) in the population. *Teleogryllus oceanicus*, is found throughout Australia and the Pacific, and since the late 1870's in the Hawaiian islands of Hawaii, Kauai and Oahu (Kevan 1990) as well, which is the only place where its range overlaps with the range of the North American parasitoid fly *Ormia ochracea* (Lehmann 2003). *O. ochracea* females locate calling *T. oceanicus* males acoustically and lay their larvae on or around them (Walker 1993). The larvae burrow in the crickets, feed on their fat body and muscle tissue, and emerge to pupate in about 7-10 days, killing the host in the process (Cade 1975).

A response to this selective pressure in Kauai and Oahu is the spread of a flatwing mutation, which renders *T. oceanicus* males unable to produce calls. This mutation has spread to more than 90% of the population in Kauai in the course of less than 20 generations (Zuk et al. 2006). Flatwing males suffer lower parasitoid-induced mortality, but since they can't produce sound and attract mates on their own they have adopted an alternative strategy – acting as satellites to calling males and intercepting females attracted to their calls (Zuk et al. 2006). This is only their first obstacle to a successful mating, because females usually mount males after they hear a courtship song, which is

different than the attraction call (Balakrishnan and Pollack 1996). Part of the solution to this problem is relaxed female preference for males. Compared to older populations, females from all Hawaiian islands have been found to be less discriminating when offered a choice between calling and silent males (Tinghitella et al. 2011), which may be due to bottlenecks during the colonization of the islands from mainland Australia and is known as the Kaneshiro effect (Kaneshiro 1989). They do, however, still prefer to mate with males producing calling and attraction songs when given the choice (Bailey et al. 2008; Tinghitella and Zuk 2009).

The populations we used were Kauai before (Kauai ancestral, or KA) and after the spread of the mutation (Kauai derived, or KD), and one from Hilo on the island of Hawaii. All have a history of exposure to the parasitoid, but flatwings have not appeared in the Hilo population. In order to test for plasticity, females from each population were reared in either silence (no song environment) or in an environment where male calls were continuously broadcast (song environment). This setup is identical to other experiments where the no song environment has reliably mimicked populations in which flatwing males are the norm (Bailey and Zuk 2008; Bailey et al. 2010; Bailey and Zuk 2012). We tested for responsiveness (time to reach a speaker broadcasting a male call), and latency to emerge from shelter after a simulated predator threat (referred to as boldness in other places in the text). Phonotactic behavior is correlated with sexual responsiveness in female crickets (Stout et al. 1976; French and Cade 1987), therefore it is an appropriate proxy for willingness to mate. Boldness was chosen, because it is one of the five main

temperament categories (Réale et al. 2007) and is often correlated with other behaviors in various studies, including some in the cricket literature, where tests similar to the one we performed to assess it have been used (Hedrick and Kortet 2006; Kortet and Hedrick 2007; Wilson et al. 2010).

We hypothesized that responsiveness would be expressed differently in the two rearing conditions (i.e. it would be plastic), such that females reared in silence would be less responsive than females reared in a song environment, because silence mimics low male density (Lloyd 1967). In the absence of constraints, we also expected females from the population with silent males (Kauai derived) to be more responsive than females from the other populations (Kauai ancestral and Hilo). Even though KA females are less discriminating when compared to females from older Hawaiian populations (Tinghitella et al. 2009), an expected consequence of the persistence of the flatwing mutation for about 10 years now (40-50 generations) is for KD females to have become more responsive to calls than the KA population. Females that are selective in this environment are theoretically less likely to find mates, and if they do, their offspring should in turn be less likely to mate given that responsiveness has a heritable component. If, on the other hand, we found evidence for constraints (correlations between behaviors with different selection pressures), it would have been possible to see no change in the level of female responsiveness before and after the mutation.



In terms of boldness, we expected to see differences between the females only in the populations/environments where the trait was correlated with other behaviors. In male *T. oceanicus* the presence of parasitoids has been shown to affect boldness. Populations with few parasitoids (Hawaii) take less time to resume calling when interrupted than populations where male mortality due to *O. ochracea* larvae is higher (Kauai ancestral) (Lewkiewicz and Zuk 2004). Furthermore, Hedrick and Kortet (2006) established that male crickets from a *Gryllus integer* population with higher predation pressure hid longer in a novel environment than did males experiencing lower predation pressure. Females, however, are affected by predation differently. Acoustically- orienting predators target predominantly males (Zuk and Kolluru 1998), and in the Hedrick and Kortet study the hiding times of females from the two populations were not significantly different.

A boldness/responsiveness syndrome was hypothesized to be present uniformly across the conditions and populations if genetic constraint models are accurate. If, on the other hand, the syndrome was present only in the Kauai ancestral population and females reared in a no song environment (it indirectly simulates greater predation pressure), or differed between the different environments and populations, this would have landed support to adaptive divergence models, unless predation pressure from other species matches *O. ochracea* pressure in other populations. Correlations between behaviors in high predation pressure settings and their absence in other conditions have been documented in several species and are considered adaptive (Bell 2005; Bell and Sih 2007; Dingemanse et al. 2007; Sih et al. 2010). Reasons include the benefit of

predictability, where consistent behavior can serve as an honest signal to predators; costs of switching between behavioral types (DeWitt et al. 1998; Dall et al. 2004; Sih et al. 2004); and tradeoffs driving selection for distinct alternative coping strategies (Stamps 2007).

## MATERIALS AND METHODS

### *Study animals*

We used *Teleogryllus oceanicus* females from 3 laboratory colonies: Hilo collected on the big island of Hawaii, initially established in 1996 (Zuk et al. 2008); Kauai ancestral (KA), established in 1991, and Kauai derived (KD), established in 2003 (Zuk et al. 2006). The colonies have been regularly supplemented with eggs from field-caught females approximately once a year, with the exception of KA, which hasn't been supplemented since 1999 (Zuk et al. 2006), when it was discovered that a mutation has rendered the majority of males in the field in this population silent. Each population before we isolated our test subjects contained more than 100 individuals to minimize the chance of inbreeding.

### *Rearing*

The females used in the two experiments outlined below were isolated from their populations when the differences between the sexes become apparent (penultimate instar) and reared individually in 118 ml cylindrical plastic containers (4.5 tall x 7cm in diameter) with ad libitum access to food (Fluker's Cricket Chow) and water. Shelter was

provided in the form of egg crates and the containers were cleaned twice a week, which is when food and water were replenished as well. The crickets were reared on a 12:12 reversed dark:light cycle at 25° Celsius, in two Precision 818 incubators, each of which was fitted with two foam lined shelves. The individual housing containers were rotated between the foam shelves after each cleaning and between the two incubators once a week to avoid incubator effects. Due to incubator capacity a maximum of 32 females from each population were housed in each at any given time. In the song environment six Sony CD players were set to play x3 average Kauai male call models, and x3 average Hilo call models. Calls were broadcast simultaneously at 70-80 dB sound pressure level (SPL) (measured at the level of the crickets) throughout the 12 hour dark part of the photoperiod (per Bailey et. al 2010). SPL was measured with an AZ Sound Meter (model 8922). Crickets in the no song environment were reared in silence. Individuals were assigned to the song or no song treatment group haphazardly.

### *Testing*

Females were tested 5-9 days post eclosion to ensure that they are sexually mature (Bailey and Zuk 2008), but avoid age as a confounding factor. Each female was tested twice, in one boldness and one responsiveness trial. The test order was determined at random and tests weren't performed on the same day to avoid stress and habituation. Individuals were weighed after each trial and the average was used for statistical analysis in order to exclude mass as a cofounding factor. After the second test the crickets were released in their populations. All boldness tests were performed 2-5 hours from the onset

of the dark part of the photoperiod and all phonotaxis trials were performed 4.5-7.5 hours after the onset of the dark part of the photoperiod to minimize any circadian rhythm effects on behavior. The temperature at the testing room was maintained at 24-25° Celsius and all tests were performed under red light.

*Experiment one: time to reach a speaker broadcasting a male call (responsiveness):*

To avoid the possibility that females from each population always prefer the calls of males from their own population, we used two synthesized male calls: an average Kauai and an average Hilo call. Before each trial, a single female was placed under an inverted 118ml plastic cup (4.5 tall x 7cm in diameter) in the middle of a 106x30cm rectangular wooden testing arena with mesh screens in the middle of the two narrow sides. A male call, randomly chosen in advance, was broadcast at 70 dB (measured at the middle of the arena), which is similar to the sound level of a calling male (Bailey et al. 2010). Two Sony SRS-M30 speakers attached to Sony CD players located behind the two mesh screens were used to broadcast the calls. Calls were initially assigned to the arena ends at random and every other testing day the CDs' positions were switched.

After 3 minutes of acclimation, during which a call was being broadcast, the cup was lifted and a timer was started. Trials were stopped if a female reached the broadcasting speaker (defined as touching the mesh directly in front of it with the antennae) in less than 7 minutes, and females that didn't were assigned the maximum score of 7 minutes (11% of 438 trials). The arena was lined with plastic in order to facilitate cleaning with

70% ethanol between trials. Cleaning was done to exclude the possibility of females getting chemical cues from the individuals tested before them. Trials where a female quickly ran towards the non-broadcasting speaker and attempted to climb out, or directly flew off of the arena (7% of 438 trials) were excluded from all data analysis, because they were likely exhibiting fleeing behavior.

*Experiment two: time to emerge from shelter after disturbance (boldness):*

Individuals were removed from their containers and placed in clean 11cm deep x 5.5cm diameter plastic cylinders (shelter), which were then placed in a novel environment (a 46x31x19cm sterilite box). After tapping on the cylinder for 30 seconds with a pencil (predator threat simulation) (Wilson et al. 2010), a timer was started and it was stopped after a female's full body emerged from the shelter. All trials were performed under red light in a temperature-regulated room (a 24-26° Celsius temperature was maintained).

The box was cleaned with 70% ethanol between trials. Individuals who didn't emerge from the cylinder in 20 minutes were given a 20 minute score - 18% of 417 trials.

Individuals who emerged in less than one minute (5% of 417 trials) were excluded from all data analysis, because they likely exhibited an escape reaction, rather than boldness.

Others (Kortet and Hedrick 2007; Wilson et al. 2010) have used acclimation periods of 1-2 minutes before the onset of trials to avoid quantifying escape behavior as latency to emerge from shelter, but since there was no acclimation time in this experiment, the one minute cutoff was used.

### *Statistical analysis*

SYSTAT v. 12 was used for statistical analysis and graphs. On the basis of modified z-scores calculated separately for each colony, 3 Hilo outliers for the responsiveness test and 3 weight outliers (modified z-scores  $>3.5$ ) were eliminated from the data set by equitable trimming. The maximum response individuals skewed the data distribution for both boldness and responsiveness. The distributions couldn't be normalized with transformations and we chose to use non-parametric tests to analyze the data.

Spearman's rank correlation tests were used to detect behavioral syndromes, which is standard in the literature (Bell 2005; Bell and Sih 2007; Hedrick and Korted 2006; Wilson et al. 2010).

*FDR corrections:* To assess the differences between the 3 populations we performed Kruskal-Wallis tests followed by multiple Mann-Whitney U tests for pairwise comparisons. Because data was re-used for these, as well as the Spearman's rank correlation tests, thus increasing the probability of type I error (rejecting a true null hypothesis), the obtained significance levels were corrected. We chose not to use Bonferroni adjustments, because they are too conservative and increase type II errors (failing to reject false null hypotheses), correcting for false discovery rates (FDR) instead (Garcia 2004).

## RESULTS

Hilo females were significantly less responsive than females from the Kauai ancestral and derived populations and also significantly less bold in both rearing environments. For all populations females reared in a song environment were significantly less responsive than females reared in a silent environment, but their boldness didn't differ significantly. A boldness/responsiveness syndrome was present in the Kauai ancestral population and both the song and no song environments.

### **Population differences:**

#### *Responsiveness:*

Hilo females were significantly less responsive than Kauai ancestral and derived females (Mann–Whitney test:  $N=280$ ,  $U=13,260$ ,  $P < 0.001$ ,  $FDR q = 0.002$ ; Table 1; fig. 1 for Hilo vs Kauai ancestral; Mann–Whitney test:  $N = 279$ ,  $U = 12,763$ ,  $P < 0.001$ ,  $FDR q = 0.002$ ; Table 1; fig. 1 for Hilo vs Kauai derived). The effect sizes for the significant results were medium (Cohen 1992; Table 1). KA and KD showed no significant differences in terms of responsiveness (Mann–Whitney test:  $N = 249$ ,  $U = 7,133.5$ ,  $P = 0.278$ ,  $FDR q = 0.334$ ; Table 1; fig. 1). The song environment did not influence these relationships (Table 1).

#### *Boldness:*

Kauai ancestral and derived females were significantly bolder than Hilo females (Mann–Whitney test:  $N = 258$ ,  $U = 10,790.5$ ,  $P < 0.001$ ;  $FDR q = 0.002$ , Table 1; fig. 2 for Kauai

ancestral vs Hilo; Mann–Whitney test:  $N = 246$ ,  $U = 9,756.5$ ,  $P < 0.001$ ;  $FDR q = 0.002$ ; Table 1; fig. 2 for Kauai derived vs Hilo), but did not differ significantly between each other (Mann–Whitney test:  $N = 228$ ,  $U = 6,457.5$ ,  $P = 0.964$ ;  $FDR q = 0.964$ ; Table 1; fig. 2). The effect sizes for the significant results were medium (Cohen 1992; see Table 1). The song environment did not influence these relationships (Table 1).

#### *Behavioral syndromes:*

A boldness/responsiveness behavioral syndrome was observed only in the Kauai ancestral population ( $N = 107$ ,  $r_s = 0.246$ ,  $P = 0.011$ ,  $FDR q = 0.032$ ; Table 3; fig. 3). When the song and no song environment were analyzed separately in KA, the statistical power was too low to detect a syndrome in either (after FDR corrections), but the correlation was much stronger in the no song environment ( $N = 47$ ,  $r_s = 0.325$ ,  $P = 0.026$ ,  $FDR q = 0.062$ ; Table 3) than the song environment ( $N = 60$ ,  $r_s = 0.133$ ,  $P = 0.311$ ,  $FDR q = 0.427$ ; Table 3).

#### **Rearing environment differences:**

##### *Responsiveness:*

Females reared in a song environment were significantly less responsive than females reared in a silent environment (Mann–Whitney test:  $N = 404$ ,  $U = 16,364$ ,  $P = 0.001$ ;  $FDR q = 0.004$ ; Table 2; fig. 4) in all populations (see Table 2). The effect size was small (Cohen 1992; see Table 2).



*Boldness:*

There was no significant difference in the expression of boldness between females reared in the two environments (Mann–Whitney test:  $N = 366$ ,  $U = 15,602$ ,  $P = 0.312$ ;  $FDR q = 0.624$ ; Table 2) in any of the populations (see Table 2).

*Behavioral syndromes:*

Behavioral syndromes were present in females reared in both the song and no song environments ( $N = 143$ ,  $r_s = 0.223$ ,  $P = 0.007$ ,  $FDR q = 0.032$ ; Table 3; fig. 5 for no song environment;  $N = 179$ ,  $r_s = 0.197$ ,  $P = 0.008$ ,  $FDR q = 0.032$ ; Table 3; fig. 6 for song environment) and the effect sizes were small (Cohen 1992; see Table 3).

## DISCUSSION

Even though a number of researchers have looked at how individuals respond behaviorally to changes in their rearing environment, including perceived predator threats (Hedrick 2000; Bell and Sih 2007; Dingemanse et al. 2007), intrasexual competition (Bailey et al. 2010), and resource/mate availability (Réale et al. 2003; Dingemanse et al. 2004; Johnson and Sih 2007), less attention has been given to the way environmental differences may influence behavioral syndromes in a sexual selection context (Jennions and Petrie 1997; Sih et al. 2004; Schuett et al. 2008; Sih et al. 2010). Here we consider how rapid environmental change (different acoustic environment due to loss of male calling ability) can influence behavioral syndromes in females from different populations. Two plastic traits were studied, one in a mating and one in a predator avoidance context.

### *Boldness*

Instances where parasitism by acoustically orienting predators changes the expression of cricket behavior have been documented, but only in males (Hedrick 2000; Lewkiewicz and Zuk 2004; Hedrick and Kortet 2006). Even though males are the primary targets of such parasitoids (Zuk and Kolluru 1998; Hedrick and Kortet 2006), female behavior could be influenced as well, since lower population densities may be an indirect signal that there are more predators present. This hypothesis was not supported here, as females from all populations had similar hiding times when reared in conditions mimicking different population densities. There is, however, a genetic component affecting boldness as well, because Hilo females were significantly shyer than females from Kauai both before and after the spread of the flatwing mutation. This difference could be due to loss of variation after a founder effect when Kauai was colonized, a correlation with responsiveness (discussed below), or it could be the result of a non-random event like different predation pressures on the two islands.

### *Responsiveness*

Female preferences for specific songs are heritable in some cricket species (Wagner et al. 1995) and Bailey and Zuk (2009) demonstrated that in *T. oceanicus*, they are plastic in regards to the social environment. Responsiveness itself was found not to be heritable in *Gryllus integer* (Gray and Cade 1999) and we found evidence that plasticity in this trait is at least partially induced by the environment in *T. oceanicus*. For all tested populations, females were significantly more responsive when reared in silence as opposed to a song

environment as expected, since silent environments signal less mating opportunities. However, we discovered population differences as well, with females from the Kauai ancestral and derived colonies being more responsive than females from Hilo in either rearing environment, which suggests that there are genetic differences between the populations as well. It is improbable that they are due to the Kaneshiro effect, because Hawaii (where the Hilo population was collected) and Kauai were colonized at similar times as evidenced by their low genetic differentiation (Tinghitella et al. 2011). Possible explanations for these population differences include founder effect, and selection for less discriminating females. While it is empirically difficult to disprove founder effect in this case, selection may have still played a role, because predation pressure from the parasitoids was strongest in Kauai (Zuk et al. 1993). Males in the KA population suffered the highest parasitoid mortality of the three (Lewkiewicz and Zuk 2004) and as a result KA females could have been driven to become more responsive to any male calls. As for KD, even though the density of males there is increasing, more than 90% of them are silent, making it impossible for females to respond to this change phonotactically. The lack of a significant difference in responsiveness between the Kauai ancestral and derived populations may also be the result of correlations with other behaviors, which are discussed in the next sub-section.

In addition, it is possible that less responsive females employ alternative strategies to find mates and don't have fewer/less fit offspring. We consider this unlikely, because even though cuticular pheromones are present in crickets (Tregenza and Wedell 1997), and do

play a role in sexual selection (Hardy and Shaw 1983; Thomas and Simmons 2009), they can only be detected at close range (Nelson and Nolen 1997). Moreover, in lab experiments, females from flatwing colonies still mate preferentially with calling males (Bailey et al. 2008; Tinghitella and Zuk 2009), so even if alternative strategies to find mates are present in silent populations, unless they are negatively correlated with responsiveness, more responsive females should still be favored by selection.

### *Behavioral Syndromes*

We found some support for adaptive divergence (syndromes change in different environments and are more likely to be present in high predation environments) behavioral syndrome models, but genetic constraints (behavioral syndromes are fixed) models can't definitively be excluded based on our results. Support for adaptive divergence from the fact that the only population in which a bold/more responsive behavioral syndrome was detected was Kauai ancestral, which suffered the highest rate of *O. ochracea* larvae infestation of the three (Lewkiewicz and Zuk 2004). It may have arisen due to plasticity as we detected no other differences between KA and KD, but genetic changes between the populations aren't completely excluded as well. If plasticity in a high predation environment induced the syndrome in KA, we expected to detect it in the females reared in silence in both populations as well, and that wasn't the case. This may be due to a small sample size making it less likely to detect existing syndromes, the fact that the silent environment isn't a perfect proxy for high predation, or the possibility that there have been genetic changes between the populations as well.

If predation has driven the formation of bold/more responsive and shy/less responsive coping styles in females in this population, such strategies could be adaptive due to a tradeoff mechanism (Dall et al. 2004; Dingemanse et al. 2007). It is possible that bold/more responsive females suffer higher predator-induced mortality, but compensate by finding mates faster and having offspring early, and shy/less responsive females have longer average lifespan than bold females, but leave fewer offspring due to later reproduction or fewer matings (see Bell and Sih 2007 and Smith and Blumstein 2010 for more examples of adaptive behavioral syndromes). These are currently only hypotheses and further research is needed to determine whether alternative strategies are indeed adaptive in *T. oceanicus* when predation is high.

While it looks like the boldness/responsiveness syndrome in KA was influenced by the environment, behavioral correlations can be caused by genetic correlations (Roff 1996; Van Oers et al. 2004) as well, and the fact that a boldness/responsiveness syndrome was present in both the song and no song environments lends some support to genetic constraint models. Our initial expectation was that if the syndrome was adaptive, it would only be present in the no song environment (which indirectly simulates high predation pressure), and that wasn't the case. However, it is also possible that boldness and responsiveness are correlated in both environments because the correlation is beneficial in both, and not due to genetic constraints. Also, in the Kauai ancestral population when the two environments were analyzed separately and a false discovery rate adjustment was applied, a syndrome was absent (no song  $FDR q = 0.062$ ; vs. song

*FDR*  $q = 0.427$ ; Table 3), but the effect size was stronger in the no song environment, where  $r_s = 0.325$  vs.  $r_s = 0.133$  in the song environment. A larger sample size would allow to determine whether there are differences in KA between the environments, and if there are, that would lend support to divergence models.

Taken together our results show that, as predicted by divergence models, a boldness/responsiveness behavioral syndrome is present in the population with highest parasitism rates, at least of *O. ochracea* - we have no reason to suspect other predation differences between the populations, especially KA and KD which come from the same spot and are only separated by a few years. The syndrome arose due to plasticity alone, or a combination of plasticity and genetic changes between the populations, which is not surprising, because selection acts on phenotypes, whether they are strictly a product of genetics, or (as is the case for most), of environment-gene interactions (West-Eberhard 1989). Both genetic constraints and adaptive divergence models could explain the fact that the syndrome was present in the song as well as the no song environments and different experiments and in some instances larger sample sizes are needed to clarify these results.

**Table 1. Population differences in boldness and responsiveness** (Mann-Whitney tests) - individuals who took <1 min to emerge from shelter and outliers were excluded. In cases where data was used for both overall and analysis of sub-groups, FDR adjustments were performed:

	Responsiveness	Responsiveness in NS	Responsiveness in S	Boldness	Boldness in NS	Boldness in S
N; df overall	404; 2	188; 2	216; 2	366; 2	167; 2	199; 2
p overall	<b>&lt;0.001</b>	<b>0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>0.001</b>	<b>0.004</b>
FDR q overall (12 tests)	<b>0.002*</b>	<b>0.002*</b>	<b>0.002*</b>	<b>0.002*</b>	<b>0.002*</b>	<b>0.006*</b>
N; df H-KA	280; 1	134; 1	146; 1	258; 1	117; 1	141; 1
p H - KA	<b>&lt;0.001</b>	<b>0.002</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>0.001</b>	<b>0.013</b>
FDR q H - KA	<b>0.002*</b>	<b>0.003*</b>	<b>0.002*</b>	<b>0.002*</b>	<b>0.002*</b>	<b>0.017*</b>
d H-KA	0.671	0.547	0.885	0.546	0.679	0.429
N; df H- KD	279; 1	132; 1	147; 1	246; 1	113; 1	133; 1
p H - KD	<b>&lt;0.001</b>	<b>0.002</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>0.004</b>	<b>0.002</b>
FDR q H - KD	<b>0.002*</b>	<b>0.003*</b>	<b>0.002*</b>	<b>0.002*</b>	<b>0.006*</b>	<b>0.004*</b>
d H- KD	0.590	0.562	0.673	0.554	0.566	0.559
N; df KA - KD	249; 1	110; 1	139; 1	228; 1	104; 1	124; 1
p KA - KD	0.278	0.336	0.435	0.964	0.555	0.617
FDR q KA - KD	0.334	0.367	0.435	0.964	0.666	0.673
d KA - KD	0.142	0.185	0.133	0.006	0.116	0.090

NS = no song environment

S = song environment

H = Hilo

KA = Kauai ancestral

KD = Kauai derived

d = Cohen's d

Significant results are bolded and significant results after FDR adjustments have a star next to them.

**Table 2. Rearing environment differences in boldness and responsiveness (Mann-Whitney tests) - in cases where data was used for both overall and analysis of sub-groups, FDR adjustments were performed:**

	N	df	d	p	FDR q-value (for 4 tests)
Responsiveness song vs no song	404	1	0.340	<b>0.001</b>	<b>0.004*</b>
Responsiveness H	155	1	0.405	<b>0.014</b>	<b>0.028*</b>
Responsiveness KA	125	1	0.382	<b>0.037</b>	<b>0.044*</b>
Responsiveness KD	124	1	0.369	<b>0.044</b>	<b>0.044*</b>
Boldness song vs no song	366	1	0.106	0.312	0.624
Boldness H	138	1	0.061	0.719	0.946
Boldness KA	120	1	0.228	0.217	0.624
Boldness KD	108	1	0.014	0.946	0.946

H = Hilo

KA = Kauai ancestral

KD = Kauai derived

d = Cohen's d

Significant results are bolded and significant results after FDR adjustments have a star next to them.



**Table 3. Correlations between boldness and responsiveness** (Spearman's rank correlation tests) – in cases where data was used for both overall and analysis of sub-groups, FDR adjustments were performed:

	N	df	$r_s$ (resp/bold)	p (resp/bold)	FDR q (resp/bold)	$r_s$ (bold/weight)	p (bold/weight)	$r_s$ (resp/weight)	p (resp/weight)	FDR q (resp/weight)
Overall	324	322	0.225	<b>&lt;0.001</b>	<b>&lt;0.001*</b>	0.103	>0.05	0.149	<b>0.007</b>	0.087
All NS	143	141	0.223	<b>0.007</b>	<b>0.032*</b>	0.104	>0.05	0.177	<b>0.033</b>	0.199
All S	179	177	0.197	<b>0.008</b>	<b>0.032*</b>	0.098	>0.05	0.101	0.179	0.428
All H	117	115	0.162	0.081	0.162	0.111	>0.05	0.166	0.074	0.234
H NS	63	61	0.195	0.126	0.215	0.155	>0.05	0.082	0.523	0.882
H S	54	52	0.093	0.504	0.604	0.036	>0.05	0.242	0.078	0.234
All KA	107	105	0.246	<b>0.011</b>	<b>0.032*</b>	0.024	>0.05	0.027	0.783	0.882
KA NS	47	45	0.325	<b>0.026</b>	0.062	0.106	>0.05	0.057	0.704	0.882
KA S	60	58	0.133	0.311	0.467	-0.054	>0.05	-0.032	0.808	0.882
All KD	100	98	0.052	0.607	0.663	0.029	>0.05	0.065	0.521	0.882
KD NS	44	42	-0.057	0.713	0.713	0.046	>0.05	0.057	0.713	0.882
KD S	56	54	0.098	0.472	0.604	0.039	>0.05	0.017	0.901	0.901

NS = no song environment

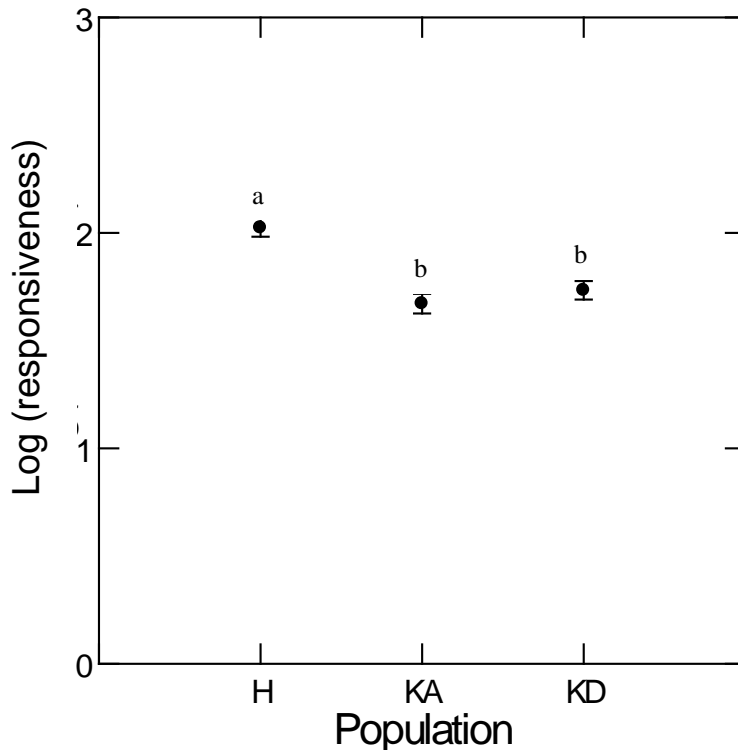
S = song environment

H = Hilo

KA = Kauai ancestral

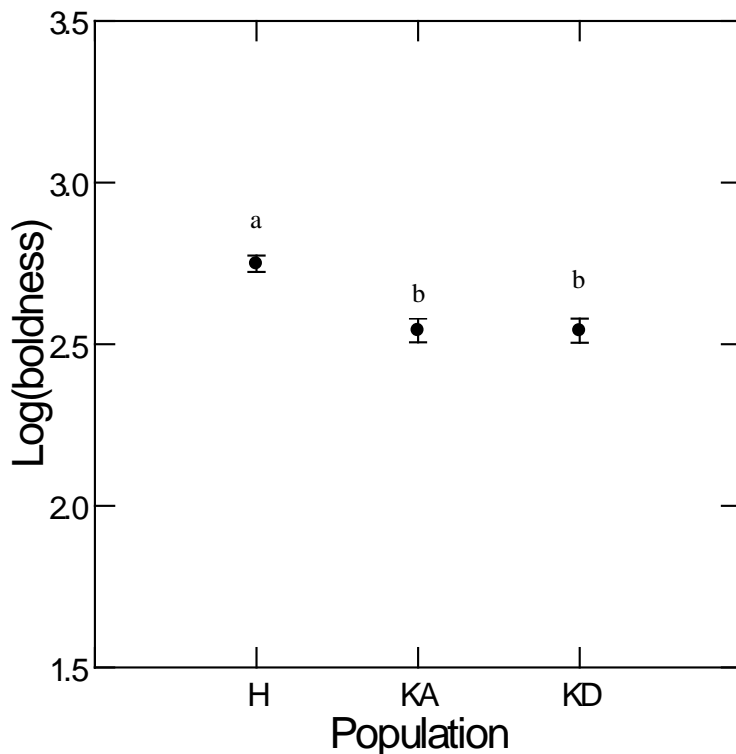
KD = Kauai derived

**Fig. 1.** Population differences in responsiveness (seconds to reach a speaker broadcasting a male call) shown with standard error bars. Mann–Whitney test:  $N=280$ ,  $U=13,260$ ,  $P < 0.001$ ,  $FDR q = 0.002$  for Hilo vs Kauai ancestral; Mann–Whitney test:  $N= 279$ ,  $U = 12,763$ ,  $P < 0.001$ ,  $FDR q = 0.002$ ; for Hilo vs Kauai derived; Mann–Whitney test:  $N= 249$ ,  $U = 7,133.5$ ,  $P = 0.278$ ,  $FDR q = 0.334$  for Kauai ancestral vs Kauai derived. Significant differences are labeled with different letters:



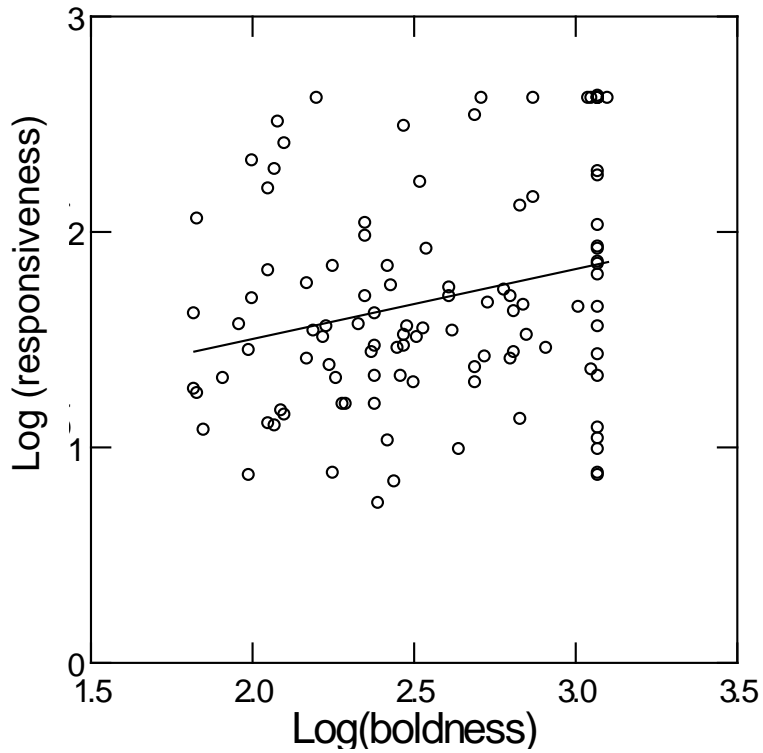
H = Hilo  
KA = Kauai ancestral  
KD = Kauai derived

**Fig. 2.** Population differences in boldness (seconds to emerge from shelter after a simulated predator threat) shown with standard error bars. Mann–Whitney test:  $N = 258$ ,  $U = 10,790.5$ ,  $P < 0.001$ ;  $FDR q = 0.002$ , for Hilo vs Kauai ancestral; Mann–Whitney test:  $N = 246$ ,  $U = 9,756.5$ ,  $P < 0.001$ ;  $FDR q = 0.002$  for Hilo vs Kauai derived; Mann–Whitney test:  $N = 228$ ,  $U = 6,457.5$ ,  $P = 0.964$ ;  $FDR q = 0.964$  for Kauai ancestral vs Kauai derived. Significant differences are labeled with different letters:

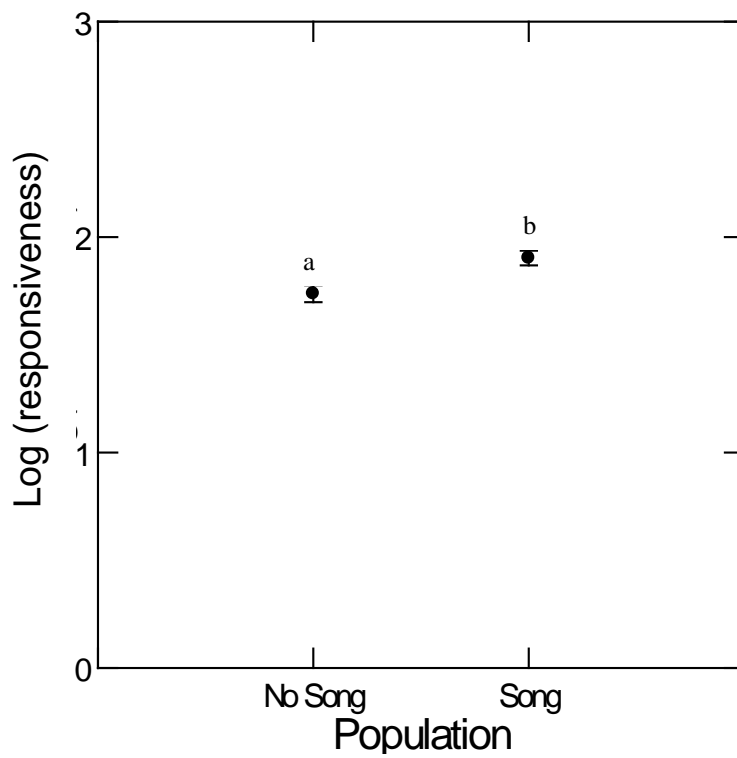


H = Hilo  
KA = Kauai ancestral  
KD = Kauai derived

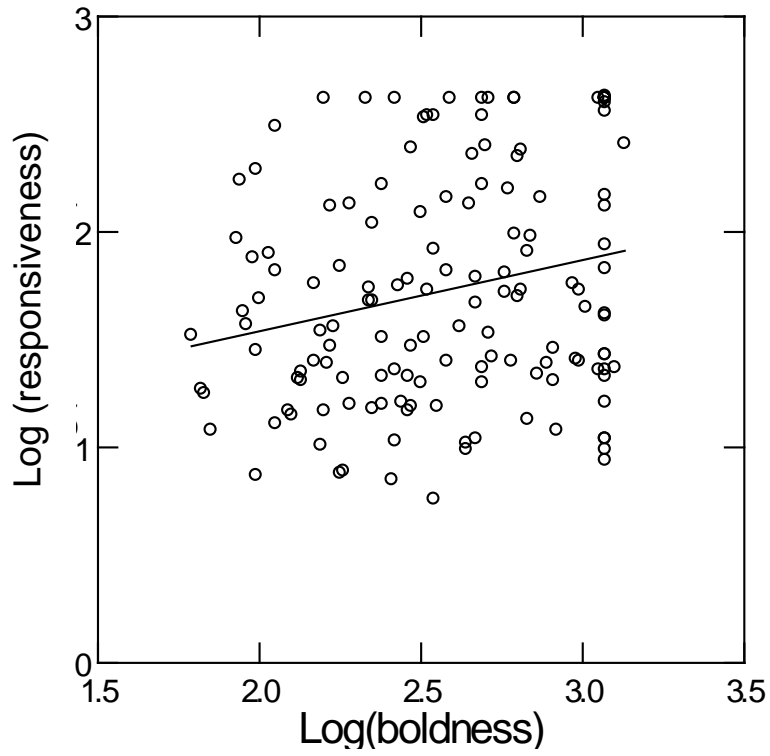
**Fig. 3.** Correlation between boldness and responsiveness in the Kauai ancestral population. Spearman's rank correlation test:  $N = 107$ ,  $r_s = 0.246$ ,  $P = 0.011$ ,  $FDR q = 0.032$ . Linear trendline fitted:



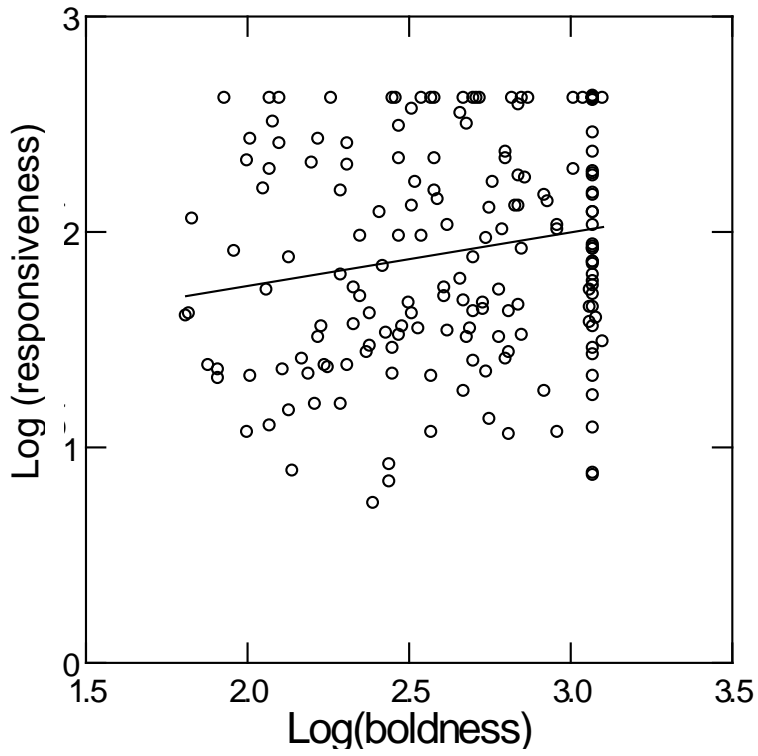
**Fig. 4.** Differences in responsiveness (seconds to reach a speaker broadcasting a male call) between environments shown with standard error bars. Mann–Whitney test:  $N = 404$ ,  $U = 16,364$ ,  $P = 0.001$ ;  $FDR q = 0.004$ . Significant differences are labeled with different letters:



**Fig. 5.** Correlation between boldness and responsiveness in the no song environment. Spearman's rank correlation:  $N = 143$ ,  $r_s = 0.223$ ,  $P = 0.007$ ,  $FDR q = \mathbf{0.032}$ . Linear trendline fitted:



**Fig. 6.** Correlation between boldness and responsiveness in the song environment. Spearman's rank correlation:  $N = 179$ ,  $r_s = 0.197$ ,  $P = \mathbf{0.008}$ ,  $FDR\ q = \mathbf{0.032}$ . Linear trendline fitted:



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