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Darwinian balancing selection: Predation counters sexual selection in a wild insect

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The potential viability costs of sexually selected traits are central to hypotheses about the evolution of exaggerated traits. Estimates of these costs in nature can come from selection analyses using multiple components of fitness during the same time frame. For a population of tree crickets (*Oecanthus nigricornis*: Gryllidae), we analyzed viability and sexual selection on male traits by comparing *Oecanthus* prey of a solitary wasp to those that survived, and comparing mating individuals to solitary males. We measured forewing width (sexually size dimorphic and used for singing), head width, pronotum length, and size of hind jumping legs as potential targets of selection. Supporting the hypothesis that sexually selected traits have viability costs, we found that significant directional sexual selection for wider heads was opposed by significant viability selection for narrower heads. Nonlinear selection revealed that individuals with wide heads and small legs were most attractive, but individuals with narrow heads, large legs, and intermediate pronotum length were most likely to survive. Successful mating may put males at greater risk of predation, especially if copulation per se is risky. Such balancing selection in tree crickets may have constrained the evolution of sexual dimorphism in head size—a condition seen in other gryllids and orthopterans.

KEY WORDS: ***Isodontia mexicana*, *Oecanthus nigricornis*, selection analysis, sexual dimorphism, viability costs.**

Darwin (1871) argued that costly extravagant traits, such as ornaments or armaments evolved because they increase mating success. In contrast, Wallace (1889) doubted whether sexually selected traits imposed survival costs (see Cronin 1991). These two perspectives have spawned formal models of female choice that represent two ends of a continuum of indirect fitness benefits to females (Kokko et al. 2002). In the Darwin–Fisher models at one end of the continuum, traits costly to survival persist because females with a preference for the trait produce attractive sons (Fisher 1930; Andersson and Iwasa 1996). These models predict that the direction of sexual selection on the trait will oppose viability (survival) selection until the two forces balance, thus preventing further elaboration of the trait (Fisher 1915). At the other end are so-called "indicator mechanism" models (Wallace's perspective: see Cronin 1991), wherein exaggerated traits reflect a male's ability to survive despite the handicap of possessing the traits (Zahavi 1975; Grafen 1990). In particular, males in better condition suffer lower survival costs (Andersson 1986). Indicator mechanism models predict that viability and sexual selection on an attractive trait will act in the same direction. During the evolution of a trait, the relationship between male trait expression and male viability may change (Eshel et al. 2000).

There is theoretical and empirical support for both the Darwin–Fisher and indicator mechanism processes (see Selander 1965; Johnstone 1995; Andersson and Iwasa 1996; Kokko et al. 2002; Mead and Arnold 2004). Although meta-analyses of empirical studies tend to support the latter in showing a mainly positive relationship between sexually selected male traits and survival (Møller and Alatalo 1999; Jennions et al. 2001; Kingsolver and Diamond 2011), negative relationships between the two have been observed, for example, in wolf spiders (Kotiaho et al. 1998), bluebirds (Keyser and Siefferman 2005), Soay sheep

(Robinson et al. 2006), and green swordtails (Hernandez-Jimenez and Rios-Cardenas 2012). Although these negative relationships are less commonly reported (Andersson and Iwasa 1996), it is premature to suggest that Darwin–Fisher processes occur less frequently in nature because many studies included in the above meta-analyses only measure adult viability, overlooking potential differential survival related to the development of attractive traits (Jennions et al. 2001). Also, some of these studies measure energetic costs rather than actual fitness costs (Kotiaho 2001). If the indicator mechanism process is more common in nature, it may reflect either that there is strong selection on females to choose attractive males that are robust enough to bear attractive traits, or that the cost of female choice is high for many species (Kokko et al. 2002). Studying examples of Darwin–Fisher selection in the wild is important to understand how components of fitness interact to produce visible phenotypes.

Demonstrations of how sexually selected traits affect survival in nature use selection analyses, a robust method of measuring selection in the wild, which determines the strength and direction of sexual and viability selection on traits (Lande and Arnold 1983). Some studies have examined contemporary viability and sexual selection on natural variation in attractive traits in wild populations (e.g., in damselflies, Svensson et al. 2004), but few have found support for the Darwin–Fisher model, particularly the predicted balancing selection between natural and sexual selection on a secondary sexual character (Kingsolver and Diamond 2011). One example was reported by Quinn et al. (2001), who found that male sockeye salmon (*Oncorhynchus nerka*) experience positive directional sexual selection for body size, but negative viability selection on body size, because large individuals more often became stranded in shallow streams or were caught by bears.

Multivariate selection analyses are especially useful in studying selection in the wild because it is likely that more than one trait contributes to survival or to attracting and securing a mate (Møller and Pomiankowski 1993; Blows et al. 2003). Multivariate selection analyses can detect linear and nonlinear selection on traits, as well as the relative contribution of that trait to fitness (Brodie et al. 1995). Nonlinear selection is often underestimated and underreported in selection studies (Blows and Brooks 2003), and although it may be more difficult to interpret, detecting nonlinear selection can indicate important evolutionary processes such as disruptive or stabilizing selection. Few studies have compared nonlinear selection from multiple components of fitness (e.g., on sperm of Mediterranean mussels [Fitzpatrick et al. 2012], on nesting traits of great tits [Garant et al. 2007]), particularly in natural populations.

Gryllid crickets (Orthoptera) have been used for sexual selection studies (Zuk and Simmons 1997) since Darwin's (1871) example of the elaborate acoustical ornament on the male forewing (tegmen)—used to attract females—and has continued with behavioral studies of male song and female preference for song (e.g., *Gryllus* and *Teleogryllus* species: Zuk 1987; Simmons 1988; Rebar et al. 2009; *Oecanthus nigricornis*: Brown et al. 1996) as well as postcopulatory behaviors such as mate guarding (e.g., Parker and Vahed 2009; Tuni et al. 2013) and nuptial feeding (e.g., Gwynne 1997; Schaus and Sakaluk 2001; Fedorka and Mousseau 2002). Studies of gryllids have shown that female preferences can impose nonlinear selection on song components (e.g., Brooks et al. 2005; Bentsen et al. 2006; Drayton et al. 2011; Oh and Shaw 2013). There is some evidence of trade-offs between attractiveness and survival. For example, song parameters of *Gryllus* species most attractive to acoustically orienting flies whose larvae kill their hosts (Cade 1975; Zuk et al. 2006) were also preferred by females—in both field (Gray and Cade 1999) and laboratory (Beckers and Wagner 2012) studies. Even in the absence of predation, there is viability selection against high-quality singing male *T. commodus*; laboratory males in high condition sing more, and thus attract more mates, "but die young" (Hunt et al. 2004). However, attractiveness does not necessarily trade-off with survival as a similar manipulative laboratory experiment with *G. pennsylvanicus* revealed that although high-condition males sang more they also lived longer (Judge et al. 2008). A similar result in a field study of *G. campestris* was attributed to variation in male quality (Rodríguez-Muñoz et al. 2010). This study also confirmed that high singing rates increased male reproductive success.

The only studies to relate mating success to survival of gryllids in the wild used life span (in part limited by predation) to estimate viability in populations of *G. campestris* (Ritz and Köhler 2010; Rodríguez-Muñoz et al. 2010). Both found evidence of directional sexual selection for larger body size (thorax width) and longevity (i.e., males that lived longer had more mates). Ritz and Köhler (2010) conducted a formal selection analysis but found no significant viability selection on the sexually selected traits of male size and condition.

Here, we use selection analyses to compare sexual selection and viability selection on wild black-horned tree crickets (*O. nigricornis,* Orthoptera: Gryllidae), using the traits tegmen width (a strongly sexually dimorphic acoustic ornament—see Fig. 1A, B), body size, head width (advantageous in male contests in related species), and hind jumping leg size (which may be beneficial in reaching mates or avoiding predators). Although the slender body form and vegetation habitats of tree crickets are different from commonly studied ground- and burrow-dwelling gryllines, *Gryllus* and *Teleogryllus,* oecanthines share many life-history traits with gryllines such as polygamy, sex differences in mate-search roles, and direct mating benefits for females (Rodríguez-Muñoz et al. 2011). Tree crickets are not known to attract acoustically orienting parasitoids (Ponce-Wainer and del Castillo 2008), but are regularly exposed to the common and widespread solitary wasp, *Isodontia mexicana* (Hymenoptera:

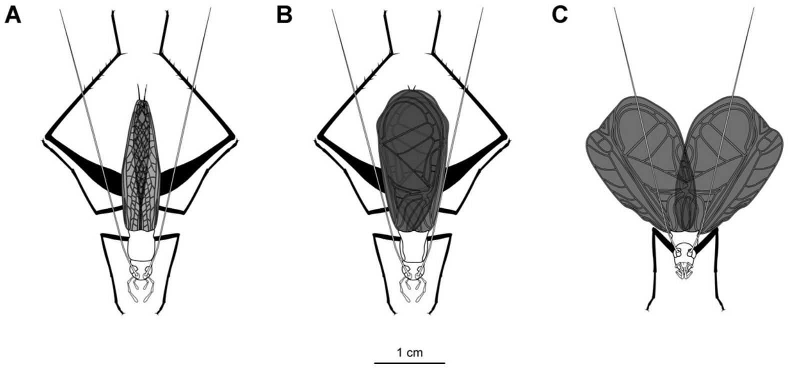

Figure 1. Adult *Oecanthus nigricornis*: (A) female, dorsal view; (B) male at rest, dorsal view; (C) male in calling posture, anterior view. (Artwork by Janice Ting.)

Sphecidae) that specializes on tree crickets and small katydids (Tettigoniidae) (Medler 1965; Iwata 1976; O'Neill 2001). Sphecid wasps sting the prey into permanent paralysis and store them as fresh provisions for offspring (an egg laid on one of the prey) (Iwata 1976; O'Neill 2001). *Isodontia* species conveniently nest in holes in wood, allowing "living dead" crickets to be easily sampled intact from artificial trap nests.

We used male survival from wasp predation and male mating success to estimate viability and sexual selection (respectively) to determine whether sexually selected traits have a positive or negative relationship with viability. If sexually attractive traits have evolved in our population of *O. nigricornis* via the Darwin–Fisher model (where sexual traits impose fitness costs that balance the mating advantage), then we predict selection on traits that improve mating success will be opposed by viability selection. Opposing selection would also be revealed in significant viability and sexual selection on multivariate axes that have similar relative contributions of traits, but where the sign of selection is opposite. If combinations of attractive traits have viability costs, then in visualizations of nonlinear selection, we expect that fitness peaks relating combinations of traits to success in one component of fitness will correspond to fitness troughs in the other. Alternatively, sexual selection and viability selection gradients that are similar in sign and form acting on the same traits or the same combinations of traits would be consistent with predictions of indicator mechanism models. If combinations of attractive traits do not have viability costs, then, in visualizations of nonlinear selection, we expect fitness peaks in both sexual and viability selection corresponding with similar combinations of traits.

Methods

STUDY ORGANISMS

The black-horned tree cricket (*O. nigricornis*) is a common singing insect in old fields of southeastern Canada and the northeastern United States (Vickery and Kevan 1985; Capinera et al. 2005). They are univoltine in Ontario, and mating occurs between mid-July and late September. Adults may live about four to six weeks (in laboratory conditions: Brown 1997) and both sexes mate as often as one to three times a day during peak mating season (early September) (Bussière et al. 2005). After a calling male attracts a receptive female, she mounts him and starts to feed on nutritious secretions (Brown 1997) from a metanotal gland between his wings at the base of his raised tegmina (Fulton 1915). If mating continues, intromission occurs and the male transfers a spermatophore, guiding it into the female's genital chamber. The female continues to feed on metanotal secretions as sperm is transferred from the spermatophore to her reproductive tract (Brown 1997). Courtship, copulation, and nuptial feeding may take 30 min or more (Brown 1997). Females have several opportunities to evaluate the quality of her mate and reject him at different stages in the courtship process (Brown 1999).

Females prefer larger males (Brown 2008) in part by using honest signals in male song (Brown et al. 1996). Such preferences may be adaptive as larger males produce higher protein gift secretions (Bussière et al. 2005). Glandular secretions can be an important resource to females because females that feed longer on the gland survived longer to lay more eggs (Brown 1997). However, male body size may not be the only important trait in sexual selection in *O. nigricornis*, as intrasexual selection has not been previously studied in tree crickets.

Our predator, *I. mexicana* takes tree cricket prey over a broad geographical range (Medler 1965; Bohart and Menke 1976; O'Neill and O'Neill 2003, 2009). Prey are carried in flight to provision nests (Iwata 1976) in naturally formed holes, rolled-up leaves, or in artificial trap-nest bores (Krombein 1967). Completed nests are sealed with a grass plug. Between seven and 20 paralyzed prey are provisioned per wasp egg, depending on the size of prey (Medler 1965). Due to the wasp's ubiquity, *I. mexicana* predation is likely a common cause of mortality in tree cricket populations. Although wasps are diurnal predators and crickets increase their mating activity late in the day and into the night, there is an overlapping period of several hours each day when both wasps are hunting, and crickets are actively courting and mating.

STUDY SITE

Our experimental site was a roughly rectangular meadow of primarily goldenrod (*Solidago* spp.), approximately 17 m by 61 m in area at the Koffler Scientific Reserve (KSR) in King City, Ontario. To facilitate the observation of mating crickets, we used a brush cutter to cut the meadow into rows of vegetation approximately 50 cm wide and 2–2.5 m apart. We removed as many tree crickets from the patch as possible before cutting, and returned them to the meadow afterward.

When most of the local cricket population had matured, we marked adult males with fluorescent powder to aid in recapturing mating crickets at night using UV lights. Initially, adult males were collected from the meadow (via net sweeping, $n = 22$) and were dusted lightly with fluorescent powder (Luminous Powder Kit, BioQuip Products, Inc., Rancho Dominguez, CA). Crickets were allowed 24–48 h to recover from the marking procedure before being returned to the meadow. In part to replace adult male crickets that we sampled over the five-week period (August 8 to September 13, 2012), we periodically released in the meadow additional marked adult male crickets collected from nearby goldenrod meadows. In total, 50 adult males were added to the meadow. Crickets were not restricted in movement into and out of the meadow.

At the northwest corner of the goldenrod patch, we placed two boxes of artificial trap nest bores (see Hallett 2001 for description). Each box was seeded with *I. mexicana* prepupa larval progeny of wasps that had nested in the trap nests the year before. Boxes contained 35 trap nests, which were pine blocks with four to six routed tunnels, and clear acrylic lids to allow inspection. Tunnels were 150 mm long, and tunnel diameters were 6.4, 8, or 9.6 mm: sizes that the wasps have been observed to use (Medler 1965).

SAMPLING

Crickets for both the sexual and viability selection analyses were sampled approximately weekly and were killed by freezing, followed by preservation in 70% ethanol. We sampled crickets for viability selection during the day and for sexual selection at after dark on the same day. Males used in the sexual selection study were not used in the viability selection study, and vice versa. For sexual selection, we estimated relative fitness using mating success. In the only field study to estimate male reproductive success in gryllids, mating success was found to be a significant determinant of lifetime reproductive success (Rodríguez-Muñoz et al. 2010). Two to four observers sampled males between 8:00 p.m. and 12:00 a.m., when calling male crickets were common, and when it was dark enough for UV lights to be used. Observers located courting males opportunistically by listening for courtship song, and located them visually using flashlights or portable UV lights. The male was collected if he was with a mounted female. After a mating male was collected, the closest (within a 2 m radius) nonmating singleton adult male was sampled for comparison, as this male was likely the closest competitor to the mating male, and was assumed to have lost in sexual competition with him. To account for possible behavioral differences in powder-marked males versus unmarked males, observers finding a marked mating male attempted to collect only a marked singleton for comparison when possible, so that marked maters were paired with marked singletons and likewise for unmarked males. For statistical analyses, mating males were assigned a fitness value of 1, and singletons were assigned a fitness value of 0. Such cross-sectional (or instantaneous) sampling can produce similar estimates of selection as longitudinal sampling (Punzalan et al. 2010; Robson and Gwynne 2010).

For the viability selection analysis, we sampled newly provisioned male tree cricket prey from *I. mexicana* trap nest bores. New prey was in distal nest cells with a wasp egg or small larva. The partially eaten remains of four crickets marked with fluorescent powder were found in *I. mexicana* nests during our sampling period, confirming that wasps were hunting from the same population from which we sampled mating, singleton, and surviving males. Due to this small number of marked crickets found in wasp nests (only four marked out of several hundred unmarked prey items), we do not believe powder-marking crickets increased their chance of getting caught. Surviving males were collected using haphazard net sweeps. In statistical analyses, survivor males were assigned a fitness value of 1, and prey males were assigned a fitness value of 0.

MEASUREMENT

Using digital photos (from an AmScope 5MP microscope digital camera mounted to a Wild Heerbrugg M5A dissecting microscope) and ImageJ software, we measured average femur length and width, and tibia length of both legs, pronotum length, tegmen width, and head width. Leg size may be important in scramble competition (e.g., Kelly et al. 2008) or escaping predation (Schulte et al. 2004); pronotum length is a common proxy for overall body size in orthopterans (Judge and Bonanno 2008; Robson and Gwynne 2010), and is strongly correlated with body mass in *O. nigricornis* (Ercit 2014); tegmina are used for singing, and are the largest visible structure (Fig. 1B, C); and head width may be important in intermale contests, as is seen in other orthopterans (Kelly 2005; Judge and Bonanno 2008). Frequency (pitch) of male calling song is important in sexual selection in *O. nigricornis* (Brown et al. 1996), but there are no known

Table 1. Relative trait loadings of leg measurements on principal component axis 1 (now called "leg size," abbreviated LS) from sexual selection and viability selection sampling.

Original trait	$PC1_S$ (sexual selection)	$PC1_V$ (viability selection)
Femur length	0.67	0.63
Femur width	0.10	0.09
Tibia length	0.74	0.77

Table 2. Descriptive statistics of traits of *Oecanthus nigricornis* males measured for sexual and viability selection analyses.

		Mean (mm) ± SEM			
Trait measurement	Abbreviation	Survivors	Prey	Maters	Singletons
Tegmen width	TW	6.64 ± 0.084	6.92 ± 0.090	6.76 ± 0.076	6.56 ± 0.093
Femur length	FL	7.89 ± 0.080	7.89 ± 0.128	7.99 ± 0.071	7.81 ± 0.106
Femur width	FW	1.35 ± 0.014	1.36 ± 0.020	1.40 ± 0.014	1.34 ± 0.019
Tibia length	TL	8.75 ± 0.108	8.75 ± 0.139	8.77 ± 0.088	8.64 ± 0.110
Pronotum length	PL	2.34 ± 0.023	2.35 ± 0.036	2.38 ± 0.021	2.30 ± 0.028
Head width	HW	1.53 ± 0.012	1.57 ± 0.015	1.58 ± 0.009	1.52 ± 0.014

morphological wing traits that reflect the variation in male song frequency (Toms 1993). Instead we assumed that because larger males have more attractive, lower frequency song (Brown et al. 1996), we would capture the variation in song frequency (and therefore attractiveness) in our pronotum length (representing body size) measurement. The measurer was blind to the relative fitness of the cricket they measured (mating, singleton, survivor, or prey).

STATISTICAL ANALYSIS

All analyses were done using R version 2.14.0 (R Development Core Team 2013). To reduce multicollinearity of the morphological traits we measured (Mitchell-Olds and Shaw 1987), we combined the three leg measurements into a single "leg size" principal component axis for both sexual and viability analyses. Principal component analysis reduced the leg measurements into a single PC axis that captured 94% of the variance in sexual selection dataset, and 96% of the variance in viability selection dataset. In both datasets, PC1 was mostly influenced by tibia length and femur length, and all leg measurements were positively loaded (Table 1). Selection analyses (Lande and Arnold 1983) were conducted, which consisted of multiple regressions of (z-score standardized) morphological measurements of male crickets against estimates of his relative survival or mating success. Linear multiple regression yielded a vector of linear selection gradients, β. These gradients can be interpreted as the strength of selection on a trait. The γ-matrix of correlational and quadratic selection gradients was obtained using multiple regressions that included all linear, quadratic, and correlational terms. Quadratic coefficients were doubled to obtain the quadratic selection gradients of the γ-matrix (Stinchcombe et al. 2008). Because estimates of fitness were binary, significance values of selection gradients were generated using multiple logistic regression (Fairbairn and Preziosi 1994; Janzen and Stern 1998). We used partial *F*-tests (Chenoweth and Blows 2005) to test if linear and nonlinear selection was different between sexual and viability selection. This consisted of comparing the unexplained sums of squares in models that did or did not include the component of selection (sexual or viability) as an explanatory variable. We also conducted a canonical analysis (Phillips and Arnold 1989) to increase the probability of detecting nonlinear selection (Blows et al. 2003). This analysis consisted of a second multiple regression on canonically rotated traits, that is, the matrix of standardized traits was multiplied by the matrix **M** (the diagonalization of the γ-matrix). We tested the significance of linear and nonlinear selection along the new axes generated by canonical rotation using multiple permutation tests (Reynolds et al. 2009), and when testing significance of eigenvalues, cross-product (in addition to quadratic) terms were added back into the model for permutation tests (Bisgaard and Ankenman 1996). To test if adding nonlinear terms explained significantly more variation than linear terms alone, we again conducted partial *F*-tests (Chenoweth and Blows 2005). We then used thin-plate splines (using the Tps function in the fields package in R) to visualize selection on the new major axes generated from canonical rotation.

Results

Sexual selection analysis included 30 mating and 31 singleton males (two singleton males were equidistant to one of the maters), and viability selection analysis compared 31 survivor and 24 prey crickets. Prey crickets were collected from nine different *I. mexicana* nests from between six and nine different wasps (wasps

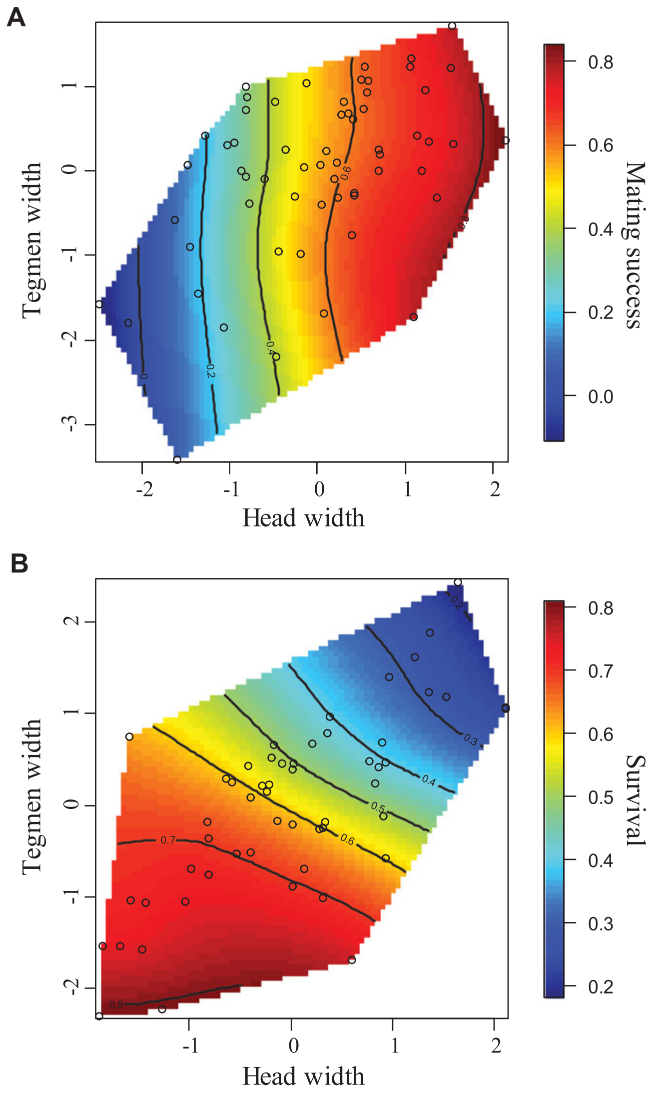

Figure 2. Colored contour plots of the relationship between estimates of (A) relative mating success of males and (B) relative survival of males and the (standardized) morphological traits head width and tegmen width. Relative mating success was determined by whether a male was found mating with a female, and relative survival was determined by if males were caught by predatory wasp *Isodontia mexicana*.

were not individually marked and often created several nests). Summary statistics of measured traits are displayed in Table 2.

Table 3. Sexual selection: vector of standardized directional selection gradients (β) and matrix of correlational and quadratic selection gradients (γ) from a sexual selection analysis on male *Oecanthus nigricornis*.

		γ-Matrix			
Trait	β	TW	LS	PL	HW
TW	0.07	−0.17	–	–	–
LS	−0.20	**0.60**	−0.20	–	–
PL	0.04	−0.09	−0.69	0.77	–
HW	**0.29**	−0.16	**0.60**	−0.33	−0.31

Bolded terms indicate significance at $\alpha = 0.05$.

Table 4. Viability selection: vector of standardized directional selection gradients (β) and matrix of correlational and quadratic selection gradients (γ) from a viability selection analysis on male *Oecanthus nigricornis*.

		γ-Matrix			
Trait	β	TW	LS	PL	HW
TW	**−0.23**	0.20	–	–	–
LS	0.16	0.14	0.16	–	–
PL	0.21	−0.16	0.07	−0.45	–
HW	**−0.26**	0.20	−0.38	−0.03	0.14

Bolded terms indicate significance at $\alpha = 0.05$.

We found significant linear sexual and viability selection on male traits (sexual $F_{4,55} = 4.101$, $P = 0.01$; viability $F_{4,49} = 4.35$, $P < 0.01$). There was significant directional sexual selection for wider heads ($\beta_S = 0.29$, $P = 0.01$) (Fig. 2A). There was no significant directional sexual selection on any other trait, but we did find significant positive correlational selection on wing width and leg size ($\gamma_S = 0.60$, $P = 0.03$), and head width and leg size ($\gamma_S = 0.60$, $P = 0.03$) (Table 3). We found significant directional viability selection for narrower heads ($\beta_V = -0.26$, $P = 0.02$) and narrower tegmina ($\beta_V = -0.23$, $P = 0.03$) (Fig. 2B). We did not detect any linear or nonlinear viability selection on any other trait or combination of traits before canonical analysis (Table 4). Directional selection on traits was significantly different between sexual and viability analyses ($F_{4,104} = 6.66$, $P < 0.001$). Both correlational and quadratic selection were not significantly different between sexual and viability analyses ($F_{6,84} = 1.82$, $P = 0.11$; $F_{4,96} = 1.79$, $P = 0.14$, respectively).

After canonical rotation, we detected significant linear sexual selection on the composite trait $\mathbf{Sm_3}$, which is most strongly influenced by head width and pronotum length, to a lesser degree ($\theta_S = 0.16$, $P = 0.03$), and $\mathbf{Sm_4}$, which contrasts leg size with head width and tegmen width ($\theta_S = 0.32$, $P = 0.02$). Adding nonlinear terms to the sexual selection model significantly improved the fit of the model ($F_{4,51} = 4.23$, $P < 0.01$). We detected significant convex sexual selection on the same composite trait $\mathbf{Sm_4}$ $\lambda_S = -1.19$, $P < 0.01$). We visualized the fitness surface described by these two major axes ($\mathbf{Sm_3}$ and $\mathbf{Sm_4}$) in a thin-plate spline (Fig. 3). In this figure we can see a fitness peak that corresponds with high values of **Sm4**, and moderately high values of **Sm3**. This peak corresponds with individuals with wide heads and small legs. The **M** matrix of eigenvectors and all corresponding eigenvalues from the sexual selection analysis are presented in Table 5.

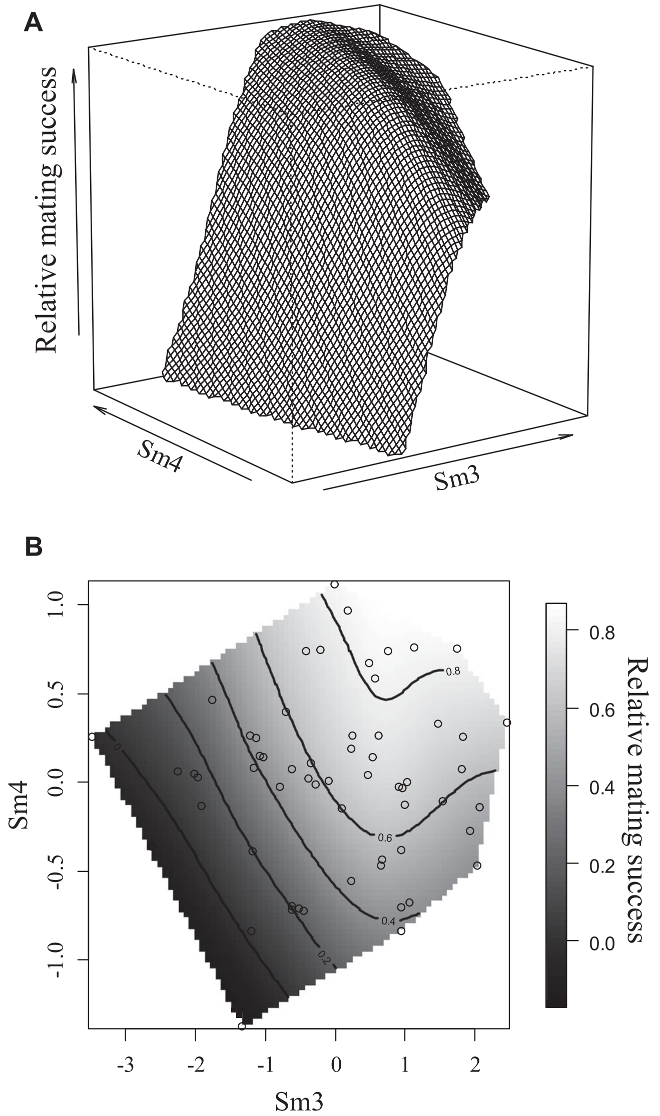

Figure 3. Thin plate spline visualization of canonical axes Sm$_3$ and Sm$_4$ from a sexual selection analysis of male tree crickets (*Oecanthus nigricornis*). (A) Perspective view, (B) contour plot. Relative fitness was estimated by whether a male was found mating with a female. The relative trait loadings of these axes are found in Table 5.

Table 5. Sexual selection: M matrix of eigenvectors and all corresponding eigenvalues.

	M matrix					
	TW	LS	PL	HW	θ	λ
Sm$_1$	−0.21	−0.52	0.76	−0.31	0.03	1.40
Sm$_2$	0.80	0.38	0.44	−0.12	−0.04	0.09
Sm$_3$	−0.27	0.30	0.45	0.79	**0.16**	−0.21
Sm$_4$	0.48	−0.70	−0.14	0.51	**0.32**	**−1.19**

Bolded terms indicate significance at $\alpha = 0.05$.

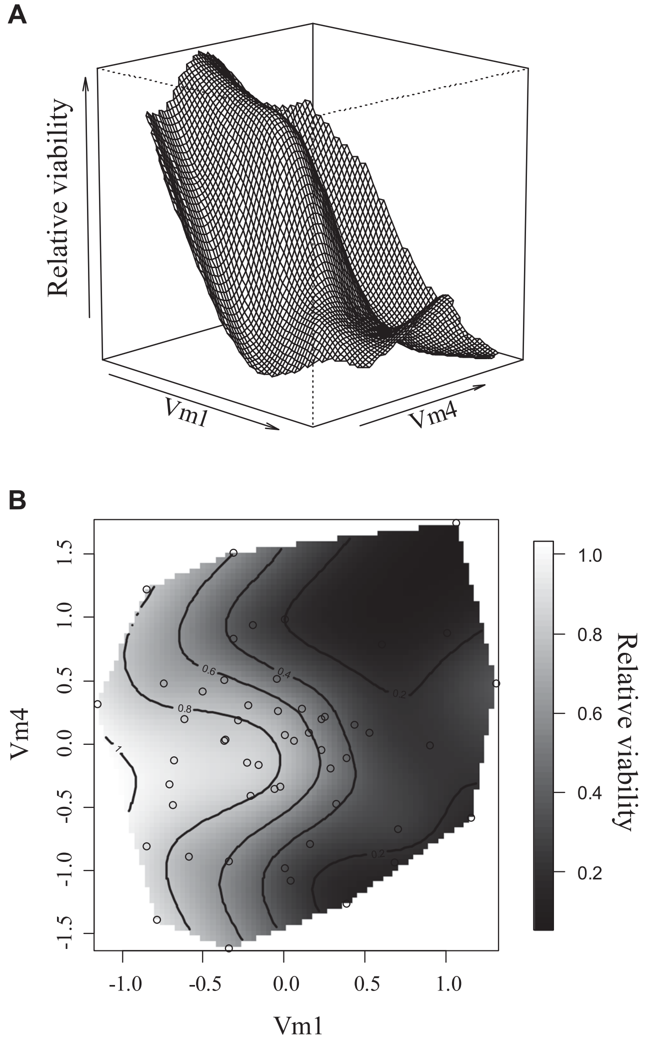

Figure 4. Thin plate spline visualization of canonical axes Vm$_1$ and Vm$_4$ from a viability selection analysis of male tree crickets (*Oecanthus nigricornis*). (A) Perspective view, (B) contour plot. Relative fitness was estimated by whether a male survived predation by a wasp, *Isodontia mexicana*. The relative trait loadings of these axes are found in Table 6.

We detected significant linear viability selection on the composite trait **Vm$_1$**, which contrasts head width and leg size ($\theta_V = -0.36$, $P = 0.01$). As with the sexual selection analysis, adding nonlinear terms to the viability selection model significantly improved the fit of the model ($F_{4,45} = 5.70$, $P < 0.001$). We found significant convex selection on composite trait **Vm$_3$**, which is fairly evenly influenced by leg size, pronotum length, and head width ($\lambda_V = -0.30$, $P < 0.001$), and on **Vm$_4$**, which represents mostly pronotum length ($\lambda_V = -0.52$, $P = 0.02$) (Fig. 4). Thin-plate spline visualization of axes **Vm$_1$** and **Vm$_4$** shows a fitness peak at low values of **Vm$_1$** and intermediate values of **Vm$_4$**, indicating that individuals with large legs, narrow heads, and intermediate pronotum lengths are most likely to survive. There are

Table 6. Viability selection: M matrix of eigenvectors and all corresponding eigenvalues.

	M matrix					
	TW	LS	PL	HW	θ	λ
Vm_1	0.20	−0.65	−0.10	0.72	**−0.36**	0.55
Vm_2	0.89	0.42	−0.15	0.12	−0.20	0.32
Vm_3	−0.28	0.56	0.44	0.64	0.08	**−0.30**
Vm_4	0.31	−0.28	0.88	−0.22	0.13	**−0.52**

Bolded terms indicate significance at $\alpha = 0.05$.

also fitness troughs at high values of **Vm_1** and extreme high and low values of **Vm_4**, which correspond with individuals with wide heads, small legs, and very long or very short pronota. The **M** matrix of eigenvectors and all corresponding eigenvalues from the viability selection analysis are presented in Table 6.

Discussion

We detected significant directional sexual selection for wider male heads. In some groups of ensiferan Orthoptera, male head width and associated mandible size is important in intrasexual competition, particularly in combat (Gryllidae: Judge and Bonanno 2008; other ensiferans: Gwynne and Jamieson 1998; Leisnham and Jamieson 2004; Kelly 2006). Our 4% difference in head width between singleton and mating males (Tables 2) is likely to be biologically relevant as Judge and Bonnano (2008) found male *G. pennsylvanicus* with only 4% wider heads (average difference in head width between winners and losers divided by average head width of all males) were significantly more likely to win in male–male combats. However, there is very little evidence of male combat in tree crickets, and female choice is likely the dominant component of sexual selection in oecanthines (Brown 1999). Larger heads and mandibles may allow for more efficient chewing, which may allow a cricket to assimilate nutrients faster, and have access to more energy for sexual displays. Because the variation in the size of morphological traits is heritable in male *O. nigricornis* (Bussière 2003), a fitness advantage for males with slightly wider heads may lead to evolutionary change over several generations, assuming low fitness costs of the trait. We did, however, find a fitness cost of head width as sexual selection for wider male heads was countered by significant viability selection for narrower heads. The magnitude of directional sexual and viability selection gradients was remarkably similar, but the direction of these gradients was opposite. We also found significant negative directional viability selection on tegmen width. The wide forewings of male tree crickets (Fig. 1B, C) encompass the complex calling modifications of this elaborate acoustical ornament (found in other singing Gryllidae: Darwin 1871), especially the sound resonating “harp” (Michelsen and Nocke 1974). Males with larger heads and wider tegmina may be at greater risk if copulation itself is risky (Magnhagen 1991), as in the *Chortoicetes terminifera* locust prey of *Sphex cognatus* wasps (Kemp 2012), where most locusts paralyzed by wasps were females but males often remained coupled to their immobilized mate as the pair was interred by the wasp (copulating locusts were observed 10 times more frequently in wasp nests than in the hunted population). Alternatively, hunting *Isodontia* may be attracted to movement of larger males during aggressive contests, calling, or courting (Burk 1982), because increased mobility (Heller 1992) and increased size (Blanckenhorn 2000 and references therein) are related to increased mortality in the wild. Surprisingly, we did not detect directional sexual selection for wider male tegmina, although we did find significant positive correlational selection on tegmen width and leg size together.

As it is likely that many traits are involved in attracting mates and predators, we also analyzed canonically rotated traits. Although selection analyses using canonical rotation were consistent with the analysis of the original traits, overall selection involved more than just directional selection on two traits. In support of the Darwin–Fisher hypothesis, composite traits under significant strong linear sexual and viability selection had similar compositions (**Sm_4** and **Vm_1**) (Tables 5 and 6), but the sign of the magnitude of selection was opposing. Both of these composite traits largely represent contributions from head width and leg size. We also found a mating success peak at moderately high values of traits **Sm_3** and **Sm_4** that corresponded with males with relatively small legs, wide heads, wide wings (Fig. 3), and these trait combinations also correspond with a viability trough at high values of **Vm_1** (wide heads and small legs) (Fig. 4). This indicates that, in our system, there is a fitness cost of having attractive combinations of traits.

The fitness surfaces reveal a complex relationship between traits and fitness. For instance, in sexual selection, an increase in trait **Sm_4** initially produces an increase in mating success, but the curvature of the fitness surface indicates that the benefit of increasing this trait diminishes (note that, even though selection on **Sm_3** appears to be strongly curved in Fig. 3, indicating stabilizing selection, nonlinear selection on this axis was not significant). There is also viability selection for individuals with intermediate values along the composite trait **Vm_4**, suggesting that there may be stabilizing viability selection on pronotum length.

Our findings are contrary to the overall trend in many other animals in which sexually attractive traits are associated with higher survival (Møller and Alatalo 1999; Jennions et al. 2001; Kingsolver and Diamond 2011). Several studies also report that directional selection is generally stronger on traits associated with mating success than traits associated with higher survival (Kingsolver et al. 2001, 2012). However, we found that the magnitude of the strength (|β|) of opposing viability and sexual selection on head width was similar. This suggests that selection on this trait is at or near equilibrium, a condition predicted by Darwin–Fisher models (Fisher 1915). Kingsolver and Diamond (2011) found that in studies of natural populations where both viability and sexual selection were measured, only 2% of cases observed such balancing selection on a trait. We acknowledge that it is difficult to determine if sexual and viability selection do indeed balance, or if head size has reached an optimum trait value, because there are many other unmeasured episodes of selection that may contribute to a male's total fitness. However we found that the sign and form of sexual and viability selection oppose each other in both univariate and multivariate analyses, which supports the conditions of the Darwin–Fisher model.

It is possible that tree cricket head width is not under direct selection, but is correlated to another trait that is under selection, such as body mass, which was not measured because of the bias caused by the mass lost by paralyzed prey. Head width thus may be correlated with the direct benefits of nuptial feeding when females choose heavyweights in this species (Brown et al. 1996; Bussière et al. 2005; Brown 2008). Like many morphological measurements, head width and body size are strongly correlated. However, we included pronotum length in our models, which is even more strongly correlated with overall body size, but did not detect any direct or indirect sexual selection on pronotum length. Head width may also be correlated to other traits such as calling rate or other song parameters.

Interestingly, in contrast to ensiferans in which males fight and there is pronounced sexual dimorphism in head and mandible size (Leisnham and Jamieson 2004; Kelly 2005; Judge and Bonanno 2008), head size is not sexually dimorphic in *O. nigricornis*. In fact, male heads are slightly smaller than those of females (K. Ercit, unpubl. data). This lack of sexual dimorphism (known for all tree crickets: Oecanthinae) may be associated with their vegetation habitat that may expose tree crickets to a higher level of predation by *Isodontia* and other wasps that commonly hunt in the vegetation. In contrast, a season-long observational study of ground-dwelling gryllines, *G. campestris*, found no wasp predation (Rodríguez-Muñoz et al. 2011), although other sphecoid wasps are known to prey on Gryllinae (O'Neill 2001).

Unlike head width, tegmen width is sexually size dimorphic in tree crickets (Fig. 1A, B), and narrow (more female-like) tegmen are likely more cryptic to visual predators. Females—lacking any stridulatory modifications—possess narrow tegmina that wrap around the slender body when perched on plant stems. It unlikely that the wasps use calling song to locate male prey because wasps take many silent juvenile crickets, and from adult populations between 69% and 92% of prey are female (O'Neill and O'Neill 2003, 2009; Ercit 2014).

Selection patterns may differ between populations (Quinn et al. 2001), and the strength of viability selection on *O. nigricornis* likely depends on the abundance of wasp predators as well as other factors. It is important to note that our measure of viability selection was from single factor, and only during a limited part of the *O. nigricornis* life cycle. As a comparison, season-long observations on reproductively active *G. campestris* crickets revealed five predator species (Rodríguez-Muñoz et al. 2011). The fact that we did find significant directional viability selection, and in approximately the same magnitude as sexual selection, despite these disadvantages is reassuring that our conservative sampling method found a biologically relevant effect.

In conclusion, we have found an unusual effect in a natural system: viability selection countered sexual selection for a male trait, possibly constraining the elaboration of a sexually dimorphic trait that is seen in related species. In the future, it is worth investigating why both Darwin–Fisher and indicator mechanism models explaining the evolution of elaborate traits can be found in nature: in some species, in some circumstances, the relationship between the direction of sexual and viability selection on a trait is positive, and in others, negative. Orthopteran systems, which display a wide variety of sexual dimorphism, patterns of mating investment, and natural enemies (e.g., Brown and Gwynne 1997; Zuk and Simmons 1997) may be useful to addressing such issues.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Table of all raw measurements and fitness scores of male *Oecanthus nigricornis* crickets used for the analyses presented in this paper. Crickets were collected from Koffler Scientific Reserve in the summer of 2012. For each sampled cricket, includes date of collection, wing width, femur length, femur width, tibia length, pronotum length, and head width measurements, relative fitness scores, and whether they were used for sexual or viability selection analyses.