Across- and Within-Population Differences in the Size and Scaling Relationship of a Sexually Selected Trait in *Leptoscelis tricolor* (Hemiptera: Coreidae)

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ABSTRACT Sexually selected traits are often assumed to convey information to conspecifics about the condition and genetic quality of an individual. However, sexually selected traits also are hypothesized to be among the most rapidly evolving and phenotypically plastic traits in natural populations. When found, such variability can bring into question the reliability of these traits as sexually-selected signals. Here, we examine the expression of a male weapon over multiple spatial and temporal scales in the wild. Specifically, we measured the expression of enlarged hind femora across and within populations of the Neotropical bug *Leptoscelis tricolor* Westwood (Hemiptera: Coreidae). We found significant variation in the size of this trait across populations and even within a population according to the plant species where adult males were collected. We also found differences in the intercept of the scaling relationship with body size; for a given body size, males in some populations express larger sexually selected traits than males in other populations. These results support the hypothesis that the expression of sexually selected traits is dynamic over space and perhaps time. Such patterns suggest that environmental variation or small amounts of movement across genetically differentiated populations may confound the reliability of information contained in the expression of these traits.

KEY WORDS allometry, sexual selection, phenotypic plasticity, microevolution, genetic differentiation

Sexual selection has resulted in some of nature's most spectacular traits, including large horns, bright coloration, and elaborate songs and dances. Allocation to these weapons and ornaments may offer strong fitness benefits in terms of reproductive success (Andersson 1994). However, elaborate trait expression often comes at a cost to survivorship (Fisher 1958, Lande 1980, Jennions et al. 2001). Thus, individuals are expected to express sexually-selected traits at a balance between natural and sexual-selection pressures (McAlpine 1979, Andersson 1982, Nur and Hasson 1984). As natural and sexual selection pressures vary across space and time, sexually selected traits are expected to evolve in their level of expression (Zuk et al. 1993, 2006; Simmons and Tomkins 1996). In fact, sexually selected traits are expected to be some of the most rapidly evolving traits in nature (Kinnison and Hendry 2001, Coltman et al. 2003, Zuk et al. 2006, Svensson and Gosden 2007).

Although genetic change (microevolution) is often assumed to be responsible for variation in sexually selected trait expression, both within and across population differences may be due to phenotypic plasticity. Sexually selected traits are often extremely environmentally sensitive (Solberg and Sæther 1994, Griffith et al. 1999, Moczek and Emlen 1999, Post et al. 1999, Qvarnström 1999, Miller and Emlen 2010). Dissimilarity in the spatial and temporal quality of resources or access to those resources may result in differences in the expression of these traits. The combination and possible interaction of microevolutionary changes and phenotypic plasticity should result in highly variable patterns of sexually selected trait expression over space and time. High lability in sexually selected traits brings into question long-held assumptions about their information content (Qvarnström 2001, Greenfield and Rodriguez 2004, Higginson and Reader 2009). Males with especially elaborate traits are often assumed to be of higher phenotypic condition and genetic quality. However, when sexually selected traits vary over space and/or time, the males expressing the most exaggerated traits may simply be, for example, those that emigrated from another population or those that experienced favorable environments within a single population. Such variation in expression may reduce the reliability of sexually selected signals and may have other important implications, including providing a resolution to the lek paradox (Miller and Moore 2007, Kokko and Heubel 2008, Radwan 2008).

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Site	 *H. hirsuta*	 *H. imbricata*	 *H. irrasa*	 *H. latispatha*	 *H. mariae*	 *H. platystachys*	 *H. pogonantha*	 *H. vaginalis*
Sherman					●			
B.C.I.			●	●	●	●		●
Gamboa			●	●	●	●		
Bocas		●			●		●	
La Selva	●	●		●	●		●	

Fig. 1. Adult insects were sampled from the following plant species at the five sites. Drawings by David Tuss.

Data on temporal changes in the expression of sexually selected traits within natural populations are relatively scarce (Solberg and Sæther 1994, Coltman et al. 2003, Garant et al. 2004, Møller and Szép 2005, Hegyi et al. 2006), and remarkably few studies have investigated natural variation in sexually selected trait expression over multiple spatial and temporal time scales. Here, we examined variation in patterns of sexually selected trait expression both across and within populations of the bug *Leptoscelis tricolor* Westwood (Hemiptera: Coreidae). We not only measured the absolute expression of a sexually selected trait but also examined the scaling relationship of this trait relative to body size. Recent work suggests that scaling relationships may evolve quickly in response to selection pressures (Wilkinson 1993, Emlen 1996, Moczek et al. 2002, Moczek and Nijhout 2003, Frankino et al. 2005). In addition, scaling relationships are now suggested to be highly phenotypically plastic (Bonduriansky and Rowe 2003, Shingleton et al. 2009, Miller and Emlen 2010), with individuals in good condition often able to express relatively larger sexually selected traits for a given body size (Cotton et al. 2004; a shift in scaling intercept). This allocation to sexually selected traits relative to body size has been suggested as a particularly potent signal to conspecific males and females of an individual's physical condition and genetic quality (Cotton et al. 2004). Thus, phenotypic variation in the sexually selected trait and/or associated body size may alter the information conveyed to others.

We measured male *L. tricolor* and estimated sexually selected scaling relationships with body size at five sites in Costa Rica and Panama. We also sampled one of these populations for four consecutive years to look for temporal changes in size and scaling. Finally, we performed an in-depth analysis at males from this population over a consecutive 4-mo period to determine whether size and scaling vary over short periods of time or according to the plant species where adult males were captured.

Methods

Study Species. *L. tricolor* has been collected from Costa Rica and Panama. Male *L. tricolor* commonly establish territories on the inflorescences of heliconia plants (Zinzerberales: Heliconiae). Males use enlarged, spiny hind femora in competition for these territories. When two males encounter one another, they often turn around, wrap their hind legs around the abdomen of the other male, and squeeze. Competitively successful males remain on a heliconia inflorescence, and unsuccessful males may hide or leave the area. Competitive behaviors such as these are common in this family of insects (Miyatake 1997, 2002, Eberhard 1998), and males with larger hind femora may be more likely to win competitions and may be more likely to mate with females present (Mitchell 1980; Fujisaki 1981; Miyatake 1993; C.W.M., unpublished data). Thus, we considered male hind femora to be sexually-selected weapons based on their involvement in male–male competitions.

Females feed and lay eggs on heliconia inflorescences and often mate with the territory-holding male. Females mate multiply and have been observed occasionally mating with small males. They lay eggs singly and may lay ≥200 eggs and continue to lay for ≥80 d (Miller 2008). Total developmental time from egg to adult is ≈40 d (C.W.M., unpublished data). Generations are overlapping, and nymphs of all stages are commonly found sharing heliconia inflorescences with adults.

Throughout the range of *L. tricolor*, and across sampling locations, diverse assemblages of heliconia plant species exist (Fig. 1). Females oviposit on many, if not

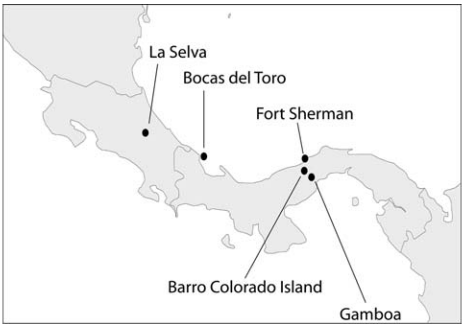

Fig. 2. Locations where insects were sampled in Panama and Costa Rica.

all, native species of heliconia, and nymphs reared on different species of heliconia develop differences in adult size, the scaling relationship of hind femora with body size, and reproductive behaviors. Moreover, these patterns differ over the course of the wet season, apparently in concert with the phenology of host plants (Miller 2007, 2008; Miller and Emlen 2010). This backdrop of environmental-sensitivity led us to predict that we would find differences in size and scaling both within and across populations.

Morphological Measurements. We traveled to five locations in Panama and Costa Rica during 2002–2005 (Fig. 2). At each location, we visited multiple stands of heliconia and measured live *L. tricolor* adult males to a maximal precision of 0.01 mm with digital calipers. We used pronotum width as a metric of body size because it is commonly used as a proxy for body size in insects and because it is easy to measure accurately due to its large size. Weapon size was measured as the mean width of the hind femurs at the third distal spine. This measurement includes both the width of the femur and the length of the spine. This area commonly contacts the abdomens of other males during male-male competitions (C.W.M., unpublished data). We attempted to only measure mature adults by excluding insects with soft cuticles (generally newly molted adults). All insects were then marked on the pronotum with nontoxic paint so as not to be resampled, and then released. Sites and years sampled are as follows: Fort Sherman, Panama (hereafter Sherman) 2002; Barro Colorado Island, Panama (hereafter B.C.I.) 2002; Gamboa, Panama (hereafter Gamboa) 2002, 2003, 2004, 2005; Isla Colon, Bocas del Toro, Panama (hereafter Bocas) 2004; and La Selva Biological Station and Reserve, Costa Rica (hereafter La Selva) 2004 (Fig. 2). All sites were sampled during the wet season in Costa Rica and Panama. The Sherman, B.C.I., and La Selva sites were sampled in the months of June and July, and the Bocas site was sampled in October. Gamboa was sampled in June and July for 2002 and 2003 and in July through October in 2004 and 2005.

Statistical Analysis. We conducted separate statistical analyses to test for effects of 1) site (five locations; $n = 314$), 2) year (within Gamboa; 4 yr; $n = 234$), and 3) month and plant species (within Gamboa 2005; 4 mo, July–October; three species; $n = 149$) on the sizes and scaling relationships between body size and male hind femur width. In addition, we tested for differences among the subset of males collected on *Heliconia mariae* Hook. f. from three sites, Sherman, Gamboa, and Bocas ($n = 121$; 10 males each from Sherman and Bocas). We did not include *H. mariae* males from B.C.I. or La Selva due to the small sample size at those sites. Analysis of variance (ANOVA) was used to test for differences in body size and hind femur width. We used analysis of covariance (ANCOVA) to test for differences in scaling slope and intercept. We first performed a separate ANCOVA to test for effects of the explanatory variable(s) on the slope of the scaling relationship between this trait and body size, indicated by a significant interaction with pronotum width. Different scaling slopes can be envisioned as nonparallel scaling relationships; one group may have a greater increase in trait size for the same increase in body size. If slopes did not significantly differ, we next examined effects of the explanatory variable(s) on the intercept of the scaling relationships (i.e., trait size when controlling for body size). All analyses were performed using both raw and log-transformed data, and they gave qualitatively similar results. Thus, we only present the analyses using the raw data. All nonsignificant interactions were removed from the final models.

Results

Site. Male *L. tricolor* differed significantly in body size ($F_{4,309} = 15.31$; $P < 0.001$; Fig. 3A) and hind femur width ($F_{4,309} = 7.48$; $P < 0.001$; Fig. 3A) across sites. Males from La Selva were on average 21% larger in body size than males from B.C.I. The slopes of the scaling relationship between body size and mean hind femur width were not significantly different across sites ($F_{4,304} = 0.54$; $P = 0.703$). Therefore, we proceeded to look for effects of site on scaling intercept. We found that the males differed significantly in the scaling intercept of hind femur width ($F_{4,308} = 4.63$; $P = 0.001$; Fig. 4). For a given body size, males from Fort Sherman had the largest hind femora, whereas males from La Selva had the smallest hind femora. Thus, although La Selva males were largest in overall size across all five sites, when body size was held constant, their investment in hind femur size was the least (Fig. 4).

Separate analyses of male *L. tricolor* collected from *H. mariae* in the Sherman, Gamboa, and Bocas sites did not reveal differences in body size ($F_{2,118} = 1.913$; $P = 0.152$) or hind femur width ($F_{2,118} = 1.117$; $P = 0.331$). Furthermore, no significant difference was found in scaling slope ($F_{2,115} = 0.485$; $P = 0.617$) or scaling intercept ($F_{2,117} = 1.852$; $P = 0.162$).

Year. Within the Gamboa site, adult males differed significantly in body size ($F_{3,230} = 3.17$; $P = 0.025$; Fig. 3B) but not hind femur width ($F_{3,230} = 2.26$; $P = 0.082$; Fig. 3B), across the years sampled. No difference was found in scaling slope across years ($F_{3,226} = 0.38$; $P = 0.767$), and we did not find a significant difference in

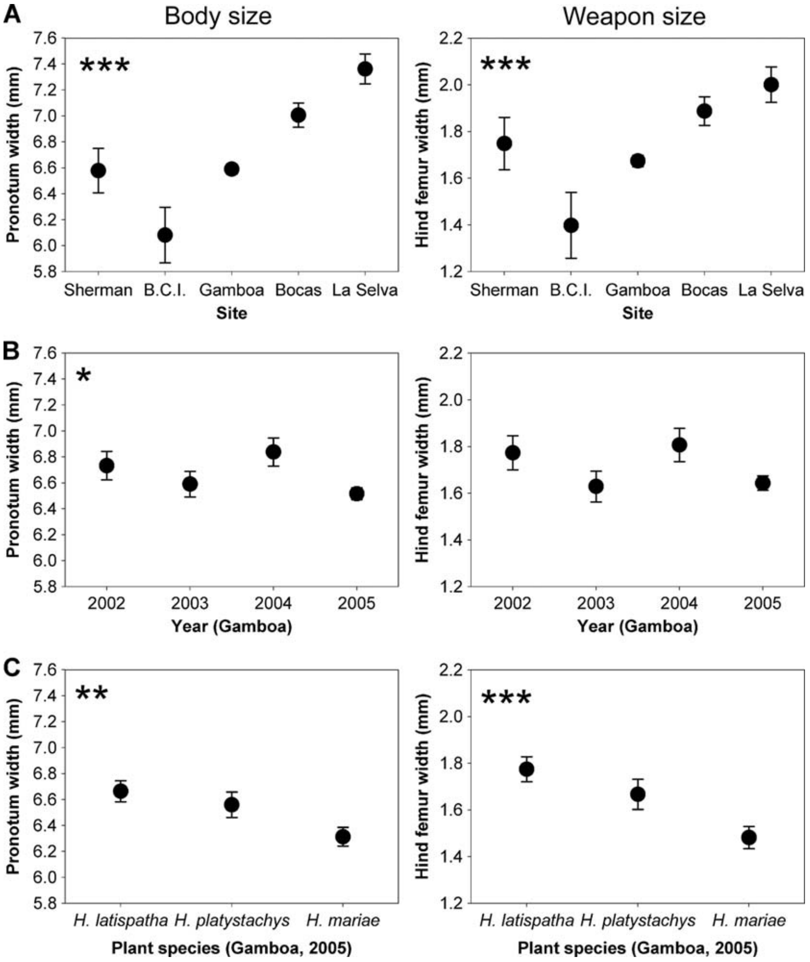

Fig. 3. Pronotum width and hind femur width according to site (A), year (for the Gamboa population) (B), and plant species (for Gamboa in 2005) (C). Least-squares estimates ± SE.

scaling intercept according to the years sampled ($F_{3,229} = 1.38$; $P = 0.251$).

Month and Plant Species. In Gamboa 2005, we did not find a significant effect of month insects were sampled on their body size ($F_{3,143} = 1.63$; $P = 0.186$; Fig. 3B), hind femur width ($F_{3,143} = 1.90$; $P = 0.132$; Fig. 3B), scaling slope ($F_{3,139} = 1.31$; $P = 0.277$), or scaling intercept of leg size on body size ($F_{3,142} = 2.21$; $P = 0.089$; Fig. 4). Furthermore, we did not find a detectable difference in the sizes of insects on each of the various plant species over the four month period ($F_{5,138} = 0.08$; $P > 0.50$). However, the plant species where adult insects were found did have a significant effect on body size ($F_{2,143} = 5.27$; $P = 0.006$; Fig. 3C) and hind femur width ($F_{2,143} = 8.19$; $P < 0.001$; Fig. 3C). The scaling slope did not differ according to plant species ($F_{2,132} = 0.78$; $P = 0.461$). We did find a significant difference in intercept ($F_{2,142} = 3.09$; $P = 0.048$; Fig. 5). Adult males collected on *Heliconia latispatha* Benth. had the widest hind legs for a given body size, and males from *H. mariae* had the narrowest (Fig. 5).

Discussion

Adult male *L. tricolor* differed in size and the scaling of their sexually selected traits according to the population and the plant species where they were collected (Figs. 3–5). These patterns support the hypothesis that sexually selected traits are phenotypically variable over multiple levels of space and time.

Across-Population Differences. Males from the Costa Rican population, La Selva, were substantially larger than males from other populations (Fig. 3A). In spite of their large overall size, males from La Selva expressed significantly narrower hind femurs at a given body size than males from the other populations (i.e., scaling relationships had the smallest intercept; Fig. 4). What could be responsible for the differences across these populations? The results shown here are consistent with our prediction that variation in the diversity and abundance of host plant species across populations should result in scaling differences. Across these five populations, the availability of heliconia species varied (Fig. 1) and thus may have in-

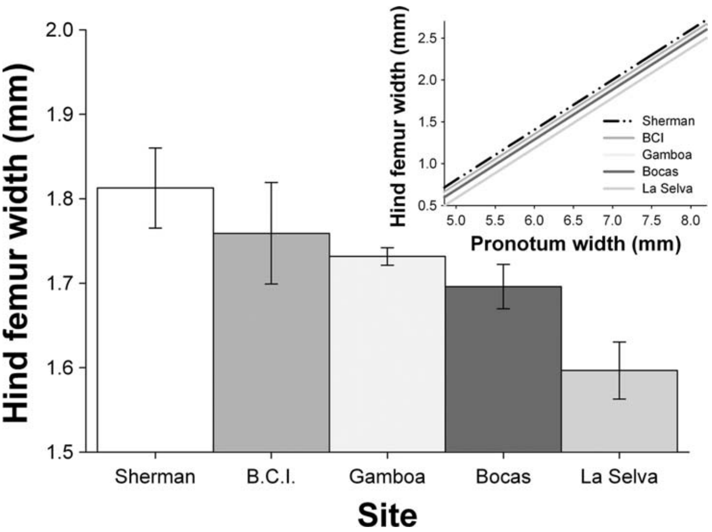

Fig. 4. Least-squares estimate ± SE of hind femur width, holding body size at the mean value across sites. Inset, predicted scaling relationships for males collected from each site.

fluenced the size and condition of the adults produced across populations. In support of this possibility, males collected solely on *H. mariae* across Gamboa, Fort Sherman, and Bocas del Toro did not differ in size or scaling relationships. However, the limited sample sizes in this latter analysis reduce the ability to make firm conclusions. Another source of variation across populations could be phenological differences of the host plants at the time that the populations were sampled (also see Miller and Emlen 2010). Finally, the possibility certainly remains that the size and scaling differences seen across populations may result at least partially from genetic differences.

Genetic variation in morphology across populations may be influenced by the costs and benefits of expressing large sexually selected traits. The density of conspecifics, availability of resources, predator assembly, and overall predation pressure are just a few common factors that may shift such costs and benefits and result in evolution of larger or smaller spiny femora. Such forces are likely responsible for microevolution in sexually selected characteristics in many species (Garant et al. 2004, Hegyi et al. 2006, Zuk et al. 2006). Indeed, variation in selection pressures have likely been important in the evolution of the incredible diversity of leg sizes and shapes in this family of insects (Coreidae), including species where males have thin hind femora similar to the legs of females, species where males have swollen femora with prominent hooks and spines, and those where females have

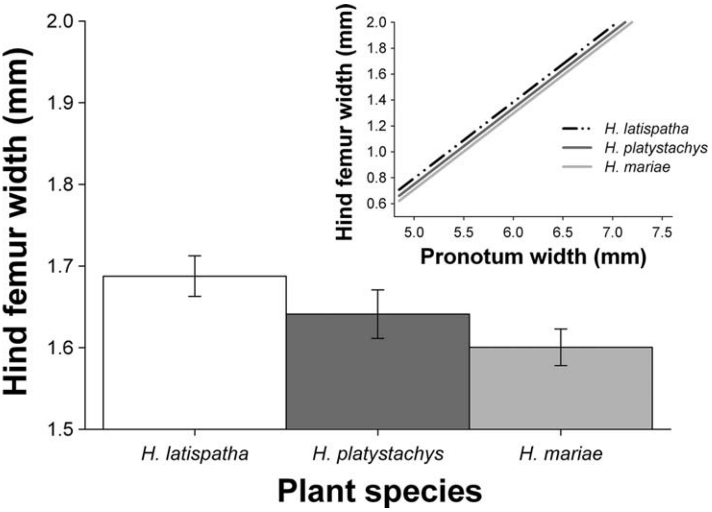

Fig. 5. Least-squares estimate ± SE of hind femur width, holding body size at the mean value across plant species. Inset, predicted scaling relationship for males collected from each plant species.

enlarged tibia that they use to defend feeding or oviposition sites (Eberhard 1998, Emlen 2008).

Within-Population Differences. We found only limited changes in morphology for insects sampled over time in the Gamboa population. We discovered across-year differences in male body size (Fig. 3B) but not in the size of hind femora or scaling relationships. In addition, we found no effect of month sampled during 2005 on adult male size and scaling. The lack of difference across months contrasts with patterns seen in offspring emerging from these different species of heliconia plants during this same time period (Miller 2007; Miller and Emlen 2010; C.W.M., unpublished data). Offspring emerging from *H. latispatha* and *Heliconia platystachys* Baker early in the season in Gamboa consistently express larger sexually selected traits and a greater scaling intercept between these traits and body size. However, later in the season, insects emerge smaller with a reduced scaling intercept. The longevity and/or frequent movement of adult insects (Miller 2007) may explain why temporal changes in offspring morphology were not reflected in adults.

We found significant within-population differences in size and scaling according to the plant species where adult males were sampled (Figs. 3 and 5). Adult males collected on *H. latispatha* were larger and expressed larger hind femora at the mean body size, whereas males from *H. mariae* were significantly smaller with relatively smaller hind femora. What could be responsible for these within-population differences?

A likely cause of this variation is carry-over effects of heliconia plant species on juveniles reared on the plants. Offspring raised on the different host plant species in this population differ significantly in adult morphology in a similar fashion as found here (Miller and Emlen 2010; C.W.M., unpublished data). The lack of detectable monthly changes in adult morphology combined with the plant species effect suggests that some adults may emerge and stay within a single patch of heliconia for multiple months. Even if a majority of adults move away from natal host plants (Miller 2007), the few remaining may be sufficient to drive the pattern observed here.

The differences in adult male size and scaling on the different host plant species may also be explained by territory quality. Because *H. latispatha* and *H. platystachys* seem to be higher quality resources for offspring production early in the wet season (Miller 2007, 2008; Miller and Emlen 2010), females may preferentially visit these plants. Males thus could benefit from flying to these high quality host plants, and those with large, spiny hind femora would probably be the most successful in maintaining a territory. Such a scenario may explain the prevalence of larger males on *H. latispatha* and *H. platystachys.* However, under this scenario it is surprising that larger males were still found on *H. platystachys* later in the wet season, given the substantial decline in the quality of these plants (Miller 2008).

Variation in Size and Scaling Relationships. The relative roles of genetic differences and phenotypic plasticity in creating the across and within-population patterns of differentiation seen here are unknown. Future studies should undertake a common garden approach with insects from multiple populations reared on several species of heliconia to examine the source of across population differences. An extensive mark–recapture study conducted in the Gamboa population would help uncover the movement patterns and longevity of adult insects, and may help explain the within population differences in size and scaling.

Results from this study suggest that sexually-selected trait expression and associated scaling relationships may commonly vary within and across populations. Such variation may easily confuse the reliability of information contained in such structures, especially when movement of animals away from natal environments is common (Greenfield and Rodriguez 2004, Bussière et al. 2008, Higginson and Reader 2009). Empirical studies are needed that combine documentation of animal movement, analyses of the sources of variation in sexually selected traits in multiple populations and/or over time, and measurement of the strength of sexual selection pressures. The consequences of changes in information content of sexually selected traits are virtually unexplored, and this will be an exciting direction for future research.

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References Cited

Andersson, M. 1982. Sexual selection, natural selection and quality advertisement. Biol. J. Linn. Soc. 17: 375–393.

Andersson, M. 1994. Sexual selection. Princeton University Press, Princeton, NJ.

Bonduriansky, R., and L. Rowe. 2003. Interactions among mechanisms of sexual selection on male body size and head shape in a sexually dimorphic fly. Evolution 57: 2046–2053.

Bussière, L. F., J. Hunt, K. N. Stölting, M. D. Jennions, and R. Brooks. 2008. Mate choice for genetic quality when environments vary: suggestions for empirical progress. Genetica 134: 69–78.

Coltman, D. W., P. O'Donoghue, J. T. Jorgenson, J. T. Hogg, C. Strobeck, and M. Festa-Bianchet. 2003. Undesirable evolutionary consequences of trophy hunting. Nature 426: 655–658.

Cotton, S., K. Fowler, and A. Pomiankowski. 2004. Do sexual ornaments demonstrate heightened condition-dependent expression as predicted by the handicap hypothesis?. Proc. R. Soc. Lond. B 271: 771–783.

Eberhard, W. G. 1998. Sexual behavior of *Acanthocephala declivis guatemalana* (Hemiptera: Coreidae) and the allometric scaling of their modified hind legs. Ann. Entomol. Soc. Am. 91: 863–871.

Emlen, D. J. 1996. Artificial selection on horn length-body size allometry in the horned beetle *Onthophagus acuminatus.* Evolution 50: 1219–1230.

Emlen, D. J. 2008. The evolution of animal weapons. Annu. Rev. Ecol. Evol. Syst. 39: 387–413.

Fisher, R. A. 1958. The genetical theory of natural selection. Oxford University Press, Oxford, United Kingdom.

Frankino, A. W., B. J. Zwann, D. L. Stern, and P. M. Brakefield. 2005. Natural selection and developmental constraints in the evolution of allometries. Science (Wash., D.C) 307: 718–720.

Fujisaki, K. 1981. Studies on the mating system of the winter cherry bug, *Acanthocoris sordidus* Thunberg (Heteroptera, Coreidae): II. Harem defense polygyny. Res. Popul. Ecol. 23: 262–279.

Garant, D., B. C. Sheldon, and L. Gustafsson. 2004. Climatic and temporal effects on the expression of secondary sexual characters: genetic and environmental components. Evolution 58: 634–644.

Greenfield, M. D., and R. L. Rodriguez. 2004. Genotype-environment interaction and the reliability of mating signals. Anim. Behav. 68: 1461–1468.

Griffith, S. C., I.P.F. Owens, and T. Burke. 1999. Environmental determination of a sexually selected trait. Nature 400: 358–360.

Hegyi, G., J. Torok, L. Toth, L. Z. Garamszegi, and B. Rosivall. 2006. Rapid temporal change in the expression and age-related information content of a sexually selected trait. J. Evol. Biol. 19: 228–238.

Higginson, A. D., and T. Reader. 2009. Environmental heterogeneity, genotype-by-environment interactions and the reliability of sexual traits as indicators of mate quality. Proc. R. Soc. Lond. B 276: 1153–1159.

Jennions, M. D., A. P. Møller, and M. Petrie. 2001. Sexually selected traits and adult survival: a meta-analysis. Q. Rev. Biol. 76: 3–36.

Kinnison, M. T., and A. P. Hendry. 2001. The pace of modern life II: from rates of contemporary microevolution to pattern and process. Genetica 112: 145–164.

Kokko, H., and K. Heubel. 2008. Condition-dependence, genotype-by-environment interactions and the lek paradox. Genetica 132: 209–216.

Lande, R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. Evolution 34: 292–305.

McAlpine, D. K. 1979. Agonistic behaviour in *Achias australis* (Diptera, Platystomatidae) and the significance of eye-stalks, pp. 221–230. *In* M. S. Blum and N. A. Blum [eds.], Sexual selection and reproductive competition in insects. Academic, New York.

Miller, C. W. 2007. Maternal effects and sexual selection in the heliconia bug, *Leptoscelis tricolor* (Hemiptera: Coreidae). Ph.D. dissertation, Division of Biological Sciences, University of Montana, Missoula.

Miller, C. W. 2008. Seasonal effects on offspring reproductive traits through maternal oviposition behavior. Behav. Ecol. 19: 1297–1304.

Miller, C. W., and A. J. Moore. 2007. A potential resolution to the lek paradox through indirect genetic effects. Proc. R. Soc. Lond. B 274: 1279–1286.

Miller, C. W., and D. J. Emlen. 2010. Dynamic effects of oviposition site on offspring sexually-selected traits and scaling relationships. Evol. Ecol. 24: 375–390.

Mitchell, P. L. 1980. Combat and territorial defense of *Acanthocephala femorata* (Hemiptera, Coreidae). Ann. Entomol. Soc. Am. 73: 404–408.

Miyatake, T. 1993. Male-male aggressive-behavior is changed by body-size difference in the leaf-footed plant bug, *Leptoglossus australis,* Fabricius (Heteroptera, Coreidae). J. Ethol. 11: 63–65.

Miyatake, T. 1997. Functional morphology of the hind legs as weapons for male contests in *Leptoglossus australis* (Heteroptera: Coreidae). J. Insect Behav. 10: 727–735.

Miyatake, T. 2002. Multi-male mating aggregation in *Notobitus meleagris* (Hemiptera: Coreidae). Ann. Entomol. Soc. Am. 95: 340–344.

Moczek, A. P., and D. J. Emlen. 1999. Proximate determination of male horn dimorphism in the beetle *Onthophagus taurus* (Coleoptera: Scarabaeidae). J. Evol. Biol. 12: 27–37.

Moczek, A. P., and H. F. Nijhout. 2003. Rapid evolution of a polyphenic threshold. Evol. Dev. 5: 259–268.

Moczek, A. P., J. Hunt, D. J. Emlen, and L. W. Simmons. 2002. Threshold evolution in exotic populations of a polyphenic beetle. Evol. Ecol. Res. 4: 587–601.

Møller, A. P., and T. Szép. 2005. Rapid evolutionary change in a secondary sexual character linked to climatic change. J. Evol. Biol. 18: 481–495.

Nur, N., and O. Hasson. 1984. Phenotypic plasticity and the handicap principle. J. Theor. Biol. 110: 275–297.

Post, E., R. Langvatn, M. C. Forchhammer, and N. C. Stenseth. 1999. Environmental variation shapes sexual dimorphism in red deer. Proc. Natl. Acad. Sci. U.S.A. 96: 4467–4471.

Qvarnström, A. 1999. Genotype-by-environment interactions in the determination of the size of a secondary sexual character in the collared flycatcher (*Ficedula albicollis*). Evolution 53: 1564–1572.

Qvarnström, A. 2001. Context-dependent genetic benefits from mate choice. Trends. Ecol. Evol. 16: 5–7.

Radwan, J. 2008. Maintenance of genetic variation in sexual ornaments: a review of the mechanisms. Genetica 134: 113–127.

Shingleton, A. W., C. M. Estep, M. V. Driscoll, and I. Dworkin. 2009. Many ways to be small: different environmental regulators of size generate distinct scaling relationships in *Drosophila melanogaster.* Proc. R. Soc. Lond. B 276: 2625–2633.

Simmons, L. W., and J. L. Tomkins. 1996. Sexual selection and the allometry of earwig forceps. Evol. Ecol. 10: 97–104.

Solberg, E. J., and B. E. Sæther. 1994. Male traits as life-history variables: annual variation in body mass and antler size in moose (*Alces alces*). J. Mammal. 75: 1069–1079.

Svensson, E. I., and T. P. Gosden. 2007. Contemporary evolution of secondary sexual traits in the wild. Funct. Ecol. 21: 422–433.

Wilkinson, G. S. 1993. Artificial sexual selection alters allometry in the stalk-eyed fly, *Cyrtodiopsis dalmanni* (Diptera: Diopsodae). Genet. Res. 62: 213–222.

Zuk, M., L. W. Simmons, and L. Cupp. 1993. Calling characteristics of parasitized and unparasitized populations of the field cricket *Teleogryllus oceanicus.* Behav. Ecol. Sociobiol. 33: 339–343.

Zuk, M., J. T. Rotenberry, and R. M. Tinghitella. 2006. Silent night: adaptive disappearance of a sexual signal in a parasitized population of field crickets. Biol. Lett. 2: 521–524.

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