Odonatologica 37(3): 221-233 *September 1, 2008*

SEXUAL SELECTION AS THE POSSIBLE UNDERLYING FORCE IN CALOPTERYGID WING PIGMENTATION: COMPARATIVE EVIDENCE WITH *HETAERINA* AND *CALOPTERYX* (ZYGOPTERA: CALOPTERYGIDAE)

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Received March 3, 2006 / Revised and Accepted January 18, 2008

Five hypotheses for the evolution of conspicuous ♂ wing pigmentation have been proposed: sexual selection, differential niche utilisation, predator warning, social badge and ecological character displacement. Here, the sexual selection and ecological character displacement hypotheses are compared. First, the coefficients of variation (CVs) of pigmentation were compared against the CVs of a selected set of other animals' traits that are known to be maintained by either natural or sexual selection. *Hetaerina americana*, *H. vulnerata*, *Calopteryx aequabilis*, *C. haemorrhoidalis* and *C. xanthostoma* were used in order to compare CVs. Second, it was predicted that pigmentation should not differ in spp. whose populations are in sympatry (compared to allopatry) if sexual selection is driving the evolution of pigmentation (compared, for example, to an ecological character displacement hypothesis in which pigmentation between spp. should differ). Here, the pigmentation of sympatric and allopatric populations of *H. americana* and *H. vulnerata* were compared. The study produced 2 main results. First, the CVs of pigmentation were not different from the CVs of sexually selected traits in other animals; nevertheless, they were different from those of naturally selected traits. Second, the pigmentation of the 2 spp. in sympatry did not differ significantly. The same was true for allopatric populations. Taken together, these results suggest that sexual selection is the main mechanism of maintenance of

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pigmentation in these animals. Other alternative hypotheses for the evolution of pigmentation (differences in habitat use in both sexes, warning to predators by ♂♂ and ecological character displacement) are discussed in the light of these results.

INTRODUCTION

Five hypotheses have been advanced to explain the evolution of exaggerated traits. (i) Sexual selection hypothesis. This is the most widely accepted and was originally proposed by DARWIN (1871) to explain the differences in morphology, physiology and behaviour between the sexes. These differences are frequently observed as exaggerated traits expressed by males. According to sexual selection theory, two processes have propelled the evolution of male exaggerated traits: (1) male-male competition over sexual access to females and (2) females choosing among males to fertilise their eggs.

(ii) Differential niche utilisation hypothesis. The sexes differ in habitat use and hence this may have produced particular adaptations to certain environments (ANDERSSON, 1994). This may be the case, for example, if both sexes differ in the places where they forage and have evolved different traits to cope with distinct needs (TEMELES et al., 2000).

(iii) Predator warning hypothesis. This hypothesis suggests that males may communicate to their predators that they are difficult targets via conspicuous traits that predators are able to recognise (BAKER & PARKER, 1979).

(iv) Social badge hypothesis. It has been suggested that conspicuous traits (e.g. colour) may act as badges that communicate an individual's social status to conspecifics (ANDERSSON, 1994). These badges would prevent unnecessary, potentially costly escalated contests over the access to resources not related to sexual reproduction or to females (reviewed by ANDERSSON, 1994).

(v) Ecological character displacement hypothesis. This assumes that exaggerated traits are species-specific traits evolved to distinguish members of other species to prevent interspecific matings in zones where the distribution of two or more species overlap (BROWN & WILSON, 1956).

Sexual selection has been studied in great detail in Odonata, particularly the Calopterygidae (reviewed by CÓRDOBA-AGUILAR & CORDERO RIVERA, 2005). Males of most species in this family develop specific wing pigmentation patterns soon after emergence (SILSBY, 2000). These patterns differ from one species to another (for example, a red basal colouration in *Hetaerina* and metallic black in *Calopteryx*) and they make males appear conspicuous. Once wing pigmentation has been developed, males establish territories where females arrive at for copulation and oviposition (CORBET, 1999). It is while defending these territories that wing pigmentation is apparently shown to conspecifics: (i) to males during the flying contests for the acquisition or defence of a territory (suggested by KOSKIMÄKI et al., 2004; RÜPPELL et al., 2005; CONTRERAS-GARDUÑO et al., 2006), and (ii) to females during the pre-copulatory flying courtship (which is the case of *Calopteryx* only; reviewed by CORDOBA-AGUILAR & CORDERO RIVERA, 2005).

Several sources of evidence in the genera *Calopteryx* (e.g. SIVA-JOTHY, 1999, 2000; CÓRDOBA-AGUILAR, 2002; CÓRDOBA-AGUILAR et al., 2003; RANTALA et al., 2000; ROLFF & SIVA-JOTHY, 2004; SVENSSON et al., 2004), *Hetaerina* (GRETHER 1996a, 1996b; CONTRERAS-GARDUNO et al., 2006) and *Mnais* (PLAISTOW & TSUBAKI, 2000; TSUBAKI & HOOPER, 2004) strongly suggest that male wing pigmentation is sexually selected. Studies have shown that highly pigmented males are usually the ones that defend a territory (e.g. GRETHER, 1996a, 1996b; SIVA-JOTHY, 2000; CÓRDOBA-AGUILAR, 2002) and they do it for longer periods (e.g. GRETHER, 1996a, 1996b; CÓRDOBA-AGUILAR, 2002) compared to less pigmented males. The underlying reason is that highly pigmented males usually have more muscular thoracic fat (CONTRERAS-GARDUÑO et al., 2006) and fewer intestinal parasites (SIVA-JOTHY, 2000; CÓRDOBA-AGUILAR, 2002). A number of studies have shown that both variables are important in territorial competition. In terms of fat reserves, they provide the necessary energetic input during territorial aerial contests (MARDEN & WAAGE, 1990; PLAISTOW & SIVA-JOTHY, 1996); in the case of parasites, they have a negative impact on fitness by affecting the elaboration of fat reserves, therefore reducing male longevity (SIVA-JOTHY & PLAISTOW, 1999). Male pigmentation has been also associated to female choice since in different *Calopteryx* species females prefer to mate with males that exhibit high levels of pigmentation (SIVA-JOTHY, 2000; CÓRDOBA-AGUILAR, 2002). Highly pigmented males actually end up having a higher lifetime mating success compared to less pigmented males (CÓRDOBA-AGUILAR, 2002).

Sexual selection, however, may not be the sole explanation for wing pigmentation in calopterygids. For instance, it is reasonable to accept that adult females and males often differ in habitat use (differential niche utilisation hypothesis). Females, for example, perch on trees or forage away from the water while males stay close to the water, mainly to defend or to compete for a territory (CORBET, 1999). Feeding can also occur in distinct places between the sexes. The predator warning hypothesis may also apply given that males exhibit themselves during territory defence and also because territories are usually open spaces where active predators, such as birds, can enter (e.g. KREBS & AVERY, 1984). The social badge hypothesis may apply only if males establish complex social groups whose members respect the owners of other territories (TRIVERS, 1985). However, this is unlikely to occur in calopterygids since territory ownership follows desperado rules: non-territorial males obtain an extremely small number of copulations; therefore males will fight until exhaustion if territories are not available (PLAISTOW & SIVA-JOTHY, 1996). Under this system, only those males that have more fat reserves will be the only ones able to defend a territory (MARDEN & WAAGE, 1990; PLAISTOW & SIVA-JOTHY, 1996). Fat reserves are correlated with wing pigmentation, therefore, it is possible that pigmentation communicates the amount of fat reserves of a given male (CONTRERAS-GARDUÑO et al., 2006). Finally, the ecological character displacement may also explain the evolution of wing pigmentation, since interspecific matings and hybrids of different calopterygid species have been observed in nature (DUMONT et al., 1987; LINDEBOOM, 1993).

In this paper we examine the potential of sexual selection to explain the evolution of pigmentation in the light of two predictions. First, according to the sexual selection theory, traits that have evolved via this selective pressure should exhibit considerably large variation in expression (when compared to characters that have evolved via natural selection, for instance; ANDERSSON, 1994). This prediction, unlike the predictions of the differential niche utilisation and the ecological character displacement hypotheses, assumes that the production of pigmentation is costly. This, however, is not the case for the predator warning hypothesis, since only males in good condition would be able to afford the production of costly traits to communicate their predators about their ability to escape (following the handicap principle; ZAHAVI & ZAHAVI, 1997). The second prediction is related to the expected pattern of pigmentation differences in allopatric versus sympatric populations. According to the ecological character displacement hypothesis, one would expect that populations (= pigmentation) of different species should be more different when in sympatry, since the risk of interspecific mating is higher in these places compared to allopatry (see an example in WAAGE, 1975, 1979). This difference, however, should not be the case if sexual selection is operating as males and females should be able to recognise non-conspecifics.

MATERIAL AND METHODS

PIGMENTATION MEASUREMENTS AND PHENOTYPIC EXPRESSION PATTERNS – The following species and locations were used: *C. aequabilis* from Canada in 1999 (N = 18), *C. haemorrhoidalis* from Spain in 1998 (N = 135), *C. xanthostoma* from Spain in 1998 (N = 28), *H. americana* from Mexico in 2000 (N = 30) and *H. vulnerata* from Mexico in 2000 (N = 24). The following conditions had to be met for the collection: 1) animals had to be sexually mature so that pigmentation was already fully developed, and 2) males had to come from the same population, preferentially being collected on the same day to avoid morphological variation caused by seasonal differences (CORBET, 1999). After capture, animals were stored in 70 % ethanol. Each individual was then placed on a petri dish containing water for two hours for tissue rehydration. Water was removed by placing every individual on a dry cloth at room temperature. Wings were cut off from their insertion to the thorax, fixed on plastic acetates and secured with transparent tape. Drawings of both total wing and pigmented areas were produced for every individual by using a stereo microscope equipped with a drawing tube (Zeiss microscope, model Stemi SV 6). Drawings were made manually at a constant distance on waxed paper. The waxed condition reduces variation in weight due to humidity. Cut outs of the pigmented and non-pigmented areas were weighed using an electronic analytical balance (OHAUS, model CT200; precision ± 0.001 g). These data were later used to estimate the percentage wing pigmentation for every individual. A similar method for measuring pigmentation has been used in previous studies and has produced reliable results (see CÓRDOBA-AGUILAR, 2002). Note that this methodology only uses degree of pigmentation but other aspects such as colour intensity are omitted. This approach is valid since it is known that the colour intensity of the pigmented patch has no sexual function in this species (CONTRERAS-GARDUÑO et al., 2007).

We obtained the coefficient of variation (CV) for pigmentation areas. CV allows data to be compared as it is expressed as a percentage (the lower the value of CV, the less variation is exhibited by the data, ZAR, 1999). We compared the CVs of pigmentation with those of traits that have evolved by sexual and natural selection from other taxa. These data were gathered from different literature sources (see Appendix 1 and Appendix 2 for a full list of these taxa and the traits used). We first checked for the distribution shape of the CVs of naturally selected traits, which did not depart from normality (Kolmogorov-Smirnov test, P = 0.58). Using the mean and standard deviation of these traits ($\mu = 4.51$, $\sigma = 1.87$), we transformed the CVs of pigmentation and those of other traits that have evolved by sexual selection in other taxa, to a standard normal distribution (ZAR, 1999). With this calculation we obtained Z scores (or units of standard deviations) for the pigmentation CVs, which allowed us to test whether these transformed values, including those of other sexually selected traits in other taxa (Fig. 1a), were likely to be found under the normal curve of naturally selected traits (Fig. 1a). This was done by checking the critical values of the proportion of the normal curve distribution in statistical tables (ZAR, 1999), which allowed us to obtain the proportion of the normal curve that lies beyond a given Z score. For example, if the P-value of a Z score of pigmentation equals or approaches zero, it means that the Z score lies outside the normal curve, therefore exhibiting a variation similar to that of sexually selected traits.

PIGMENTATION VARIATION IN ALLOPATRIC AND SYMPATRIC POPULATIONS – The following specimens were collected in 2000 in Mexico: *H. americana* (N = 20) from Jiutepec, Morelos (allopatric population), *H. vulnerata* (N = 20) from Xalapa, Veracruz (allopatric population), *H. americana* (N = 20) and *H. vulnerata* (N = 20) from Jiutepec, Morelos (sympatric populations). The collecting conditions were the same as indicated above. Since the males of all these species share similar patterns (a red basal spot on the basis of each wing), the extent of pigmentation was measured as the longitudinal length of the spot (from the wing base outwards). The mean pigmentation sizes of allopatric and sympatric populations were tested using t-tests.

Data are provided as means ± STD unless stated otherwise.

RESULTS

PHENOTYPIC EXPRESSION OF PIGMENTATION

The CVs of pigmentation (*C. aequabilis* = 13.02%, *C. haemorrhoidalis* = 14.89%, *C. xanthostoma* = 19.70%, *H. americana* = 14.44%, *H. vulnerata* = 13.06%) fell outside the curve of traits shaped by natural selection (Fig. 1b), which is similar to that which occurs to sexually selected traits in other taxa (compare Figs 1a, b). This exclusion was statistically significant in all species (Tab. I).

PIGMENTATION IN ALLOPATRIC AND SYMPATRIC POPULATIONS

There were no significant differences between the lengths of the pigmented patches in allopatric ($t_{38} = -1.58$, $P = 0.120$) or sympatric populations ($t_{38} = 0.95$, $P = 0.350$).

DISCUSSION

Our results indicate that in a selected subset of *Calopteryx* and *Hetaerina* species as representatives of Calopterygidae, evidence supports a sexual selection explanation for the maintenance of wing pigmentation, a common trait shared by most members of this family. Members of these two genera have been traditionally used to test sexual selection assumptions and actually it is mainly from *Calopteryx* where evidence for this theory is stronger (reviewed in CORDOBA-AGUILAR & CORDERO RIVERA, 2005). In *Calopteryx* and *Hetaerina*, the phenotypic expression of wing pigmentation is more similar to the expression of those traits that have been shaped by sexual selection, rather than it is to the expression of those traits shaped by natural selection in other taxa. Note that the list of traits we used came from very different animals (see Appendix 1 & 2). Given this, and the large sample of species used, it is unlikely that our results are due to chance. We also tested whether pigmentation differed more in sympatric than in

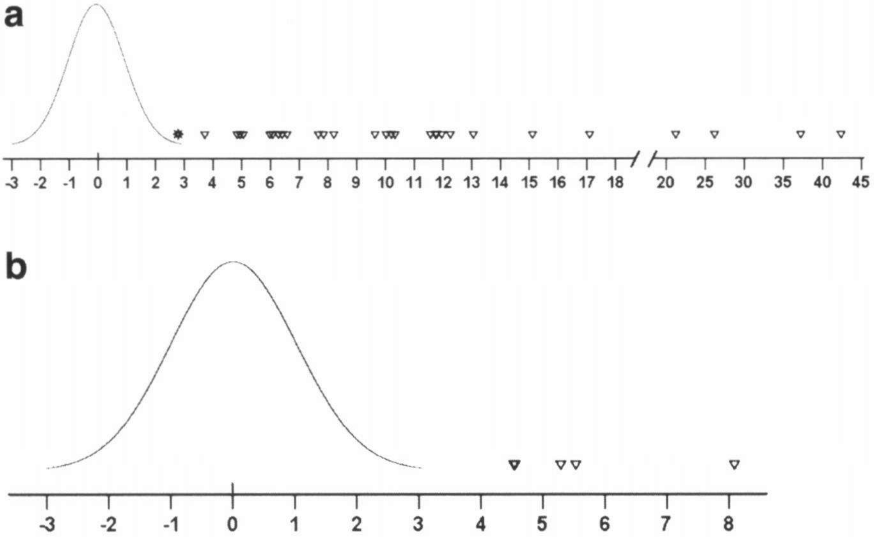

Fig. 1a: Distribution of traits under natural and sexual selection in non-odonate species (see Appendix 1 and 2 respectively). The normal curve represents the distribution of the CVs of naturally selected traits and zero denotes the mean. Numbers are standard deviations. Note that up to 98% of the values of the CVs of traits under natural selection are included within ± 3 standard deviations. Due to higher variation, most of the traits under sexual selection (inverted triangles) fall outside the normal distribution curve and more than 3 standard deviations away from the mean (except for the extreme value noted by an asterisk). — Fig. 1b: Normal distribution curve of the CVs of traits under the influence of natural selection. Zero denotes the mean; numbers are standard deviations. Inverted triangles represent the Z scores of the CVs of pigmentation.

allopatric populations. We assumed that in sympatric populations, the expression of pigmentation should differ considerably among species if a process of ecological character displacement was acting on the pigmentation patterns. Contrary to this process, we found that the pigmentation size in the two *Hetaerina* species did not differ in sympatric or allopatric populations. This clearly means that, if ecological character displacement is operating, the selected trait that males and/or females will recognise is not the pigmentation.

For our first prediction (the phenotypic expression of wing pigmentation, see Introduction), we believe it is unlikely that the differential niche utilisation hypothesis provides an explanation to our results, mainly because there would be no point in producing a male trait that is very costly. Also, although mature males and females often occupy different areas, teneral and fully mature non-territorial males may also forage away from territories (KIRKTON & SCHULTZ, 2001), in areas where females can also be found foraging. The predator warning hypothesis may apply as long as pigmentation has evolved to become an honest character that not all individuals are able to produce, so that the information provided to predators is a guarantee that the animal is able to escape if chased. The likely predators of most dragon- and damselflies are birds and other insects that are actively searching for prey (reviewed by CORBET, 1999). Given that pigmentation correlates with fat reserves (so that males with more pigmentation can devote more energy to flying (CONTRERAS-GARDUÑO et al., 2006)), it is possible that more pigmented males are better at evading a predator. This, however, has not been tested. This hypothesis assumes that predators forage only where males are present. Although there is evidence that some bird species specialize in eating odonates (e.g. KENNEDY, 1950; BAGG, 1958), to our knowledge, no study has documented a male bias in dragonfly predation by these predators.

Our results are incompatible with the ecological character displacement hypothesis. Other studies in *H. americana* have suggested that males use the pigmented patch when competing over territories. These studies have found that males with more pigmentation are more likely to win fights (KÖSKIMAKI et al., 2004;

Table I

Coefficients of variation of wing pigmentation, Z scores and the proportion of the area that lies beyond these scores. P values reflect how likely it is that the expression of pigmentation values fall outside the distribution of natural selection characters

Species	CVs of WP	Z Score	P
Calopteryx aequabilis	13.02	4.53	$P < 0.001$
Calopteryx haemorrhoidalis	14.89	5.53	$P < 0.001$
Calopteryx xanthostoma	19.70	8.09	$P < 0.001$
Hetaerina americana	14.44	5.29	$P < 0.001$
Hetaerina vulnerata	13.06	4.55	$P < 0.001$

CONTRERAS-GARDUNO et al., 2006). This possibly means that combatants recognise each other's fighting potential based on the information transmitted by the pigmentation size patterns (see SERRANO-MENESES et al., 2007). On the other hand (and contrary to this recognition idea), recent work on *C. virgo* and *C. splendens* has shown that, when in sympatry, the former species can be more aggressive towards the latter, often displacing it (TYNKKYNEN et al., 2004). Aggression is more directed against *C. splendens* males, since males of this species exhibit large wing pigmentation spots that resemble the pigmentation patterns of *C. virgo*. This lack of recognition of heterospecifics is somehow similar to what WAAGE (1975, 1979) has detected in *C. maculata* and *C. aequabilis*, where female pigmentation was different in sympatric situations compared to allopatric situations. Paradoxically, it is females and not males that have evolved different pigmentation patterns to avoid interspecific matings so males would discriminate among homo- and heterospecific females. Interestingly, evidence from *C. xanthostoma* males suggests that they are able to recognize female mates from non mates (HOOPER, 1995). In odonates, in general, it is not clear whether, and to what extent, males can recognize homo- and heterospecifics since it seems that not all species have this ability (even in species within the same genus; reviewed by CORBET, 1999). Given the potential costs of unnecessary fights by males and of matings with females, this field deserves further research. What seems a reasonable suggestion for the origin of pigmentation with respect to the ecological character displacement hypothesis, is that pigmentation, given its production costs, arose via sexual selection and possibly is now being shaped by other evolutionary forces such as the interspecific male-male aggression observed in *Calopteryx* (TYNKKYNEN et al., 2004, 2005).

Finally it should be noted that our pigmentation measurements have been based on size only. However, given the fact that odonates can see ultraviolet patterns (CORBET, 1999), the potential exists for using this as a mean for communication and this deserves further investigation.

ACKNOWLEDGEMENTS

Thanks are due to the Royal Society and Academia Mexicana de Ciencias for a grant provided to AC-A, for a short visit to the United Kingdom.

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APPENDIX 1

Coefficients of variation of naturally selected traits, Z scores and the proportion of the normal curve that lies beyond a given Z score. Sources: (1) ARNQVIST, 1992; (2) BADYAEV & HILL, 2000; (3) BADYAEV & MARTIN, 2000; (4) BADYAEV et al., 2000; (5) COHN, 1990; (6) FAIRBAIRN & PREZIOSI, 1996; (7) FORSLUND, 2000; (8) LOFTUS-HILLS & LITTLEJOHN, 1992; (9) PRYKE et al., 2001

Taxonomic group	Trait	CV (%)	Z score	P	Source
Aquarius remigis (Heteroptera, Gerridae)	Total length	4.21	-0.16	0.436	6
Aquarius remigis (Heteroptera, Gerridae)	Prefemoral width	4.81	0.16	0.436	6
Aquarius remigis (Heteroptera, Gerridae)	Mesofemoral width	4.64	0.06	0.476	6
Carpodacus mexicanus (Aves, Fringillidae)	Culmen length	5.42	0.48	0.315	3
Carpodacus mexicanus (Aves, Fringillidae)	Wing length	2.25	-1.21	0.115	3
Carpodacus mexicanus (Aves, Fringillidae)	Body mass	7.09	1.37	0.085	3
Carpodacus mexicanus (Aves, Fringillidae)	Culmen length	3.52	-0.53	0.298	2
Carpodacus mexicanus (Aves, Fringillidae)	Wing length	2.46	-1.09	0.137	2
Carpodacus mexicanus (Aves, Fringillidae)	Tarsus length	3.15	-0.73	0.232	2
Carpodacus mexicanus (Aves, Fringillidae)	Body mass	6.45	1.03	0.151	2
Carpodacus mexicanus (Aves, Fringillidae)	Culmen length	4.02	-0.26	0.397	4
Carpodacus mexicanus (Aves, Fringillidae)	Wing length	2.44	-1.11	0.133	4
Carpodacus mexicanus (Aves, Fringillidae)	Tarsus length	3.50	-0.54	0.294	4
Carpodacus mexicanus (Aves, Fringillidae)	Body mass	5.89	0.73	0.232	4
Euplectes ardens (Aves, Ploceidae)	Collar area	8.35	2.04	0.020	9
Euplectes ardens (Aves, Ploceidae)	Culmen length	2.66	-0.99	0.161	9
Euplectes ardens (Aves, Ploceidae)	Tarsus length	1.31	-1.71	0.043	9
Euplectes ardens (Aves, Ploceidae)	Wing length	1.63	-1.54	0.061	9
Euplectes ardens (Aves, Ploceidae)	Body mass	5.36	0.45	0.326	9
Forficula auricularia (Dermaptera, Forficulidae)	Elytra width	5.87	0.72	0.235	7
Forficula auricularia (Dermaptera, Forficulidae)	Elytra length	8.73	2.25	0.012	7
Forficula auricularia (Dermaptera, Forficulidae)	Pronotum width	7.17	1.41	0.079	7
Gastrophryne olivacea (Anura, Microhylidae)	Body length	7.14	1.39	0.082	8
Gastroprhyne olivacea (Anura, Microhylidae)	Body length	5.41	0.48	0.315	8
Gerris odontogaster (Heteroptera, Gerridae)	Length of middle legs	2.95	-0.84	0.200	1
Gerris odontogaster (Heteroptera, Gerridae)	Length of middle legs	3.37	-0.61	0.270	1
Gerris odontogaster (Heteroptera, Gerridae)	Length of middle legs	3.56	-0.51	0.305	1
Gerris odontogaster (Heteroptera, Gerridae)	Length of anterior femur	3.22	-0.69	0.245	1
Gerris odontogaster (Heteroptera, Gerridae)	Length of anterior femur	3.27	-0.67	0.251	1
Gerris odontogaster (Heteroptera, Gerridae)	Length of anterior femur	4.37	-0.08	0.468	1
Gerris odontogaster (Heteroptera, Gerridae)	Elytra width	4.04	-0.26	0.397	1
Gerris odontogaster (Heteroptera, Gerridae)	Elytra width	3.06	-0.78	0.217	1
Gerris odontogaster (Heteroptera, Gerridae)	Elytra width	3.03	-0.79	0.214	1
Nephila clavipes (Aranae, Araneidae)	Palp length	5.33	0.43	0.333	5
Nephila clavipes (Aranae, Araneidae)	Conductor length	4.91	0.21	0.416	5
Nephila clavipes (Aranae, Araneidae)	Conductor length	4.90	0.20	0.420	5
Nephila clavipes (Aranae, Araneidae)	Conductor width	7.71	1.70	0.044	5

APPENDIX 2

Coefficients of variation (CV) of sexually selected traits, Z scores and the proportion of the normal curve of naturally selected traits that lies beyond a given Z score. Sources: (1) BADYAEV & YOUNG, 2004; (2) FAIRBAIRN & PREZIOSI, 1996; (3) FORSLUND, 2000; (4) KLAPPERT & REINHOLD, 2003; (5) LÜPOLD et al., 2004; (6) MARKOW et al., 1996; (7) MØLLER & PETRIE, 2002; (8) PRYKE et al., 2001; (9) REGOSIN & PRUETT-JONES, 2001; (10) REID et al., 2005; (11) WARNER & SCHULTZ, 1992

Taxonomic group	Trait	CV (%)	Z score	P	Source
Aquarius remigis (Heteroptera, Gerridae)	Wing shape	74.34	37.24	0.000	2
Carduelis flammea (Aves, Fringillidae)	Visible area of ornamentation	36.60	17.11	0.000	1
Carduelis flammea (Aves, Fringillidae)	Hue (ornamentation)	16.30	6.28	0.000	1
Carpodacus mexicanus (Aves, Fringillidae)	Visible area of ornamentation	29.00	13.06	0.000	1
Carpodacus mexicanus (Aves, Fringillidae)	Hue (ornamentation)	18.90	7.67	0.000	1
Chorthippus biguttulus (Orthoptera, Acrididae)	Attractiveness of two-leg males	44.33	21.23	0.000	4
Chorthippus biguttulus (Orthoptera, Acrididae)	Loudness of two-leg males	26.94	11.96	0.000	4
Chorthippus biguttulus (Orthoptera, Acrididae)	Pause/syllable ratio of two-leg males	19.23	7.85	0.000	4
Drosophila pseudoobscura (Diptera, Drosophilidae)	Bristle number of mating males	15.74	5.98	0.000	6
Drosophila pseudoobscura (Diptera, Drosophilidae)	Upper sex comb of mating males	23.67	10.21	0.000	6
Drosophila pseudoobscura (Diptera, Drosophilidae)	Lower sex comb of mating males	53.67	26.21	0.000	6
Drosophila simulans (Diptera, Drosophilidae)	Bristle number of mating males	15.92	6.08	0.000	6
Drosophila simulans (Diptera, Drosophilidae)	Sex comb number of mating males	9.75	2.79	0.002	6
Euplectes ardens (Aves, Ploceidae)	Tail length	16.85	6.58	0.000	8
Forficula auricularia (Dermaptera, Forficulidae)	Forceps length	19.92	8.21	0.000	3
Forficula auricularia (Dermaptera, Forficulidae)	Abdomen length	16.54	6.41	0.000	3
Forficula auricularia (Dermaptera, Forficulidae)	Body mass	26.20	11.57	0.000	3
Melospiza melodia (Aves, Emberizidae)	Song repertoire size	22.60	9.64	0.000	10
Nyctalus noctula (Chiroptera, Vespertilionidae)	Penis length	11.50	3.72	0.000	5
Passer domesticus (Aves, Passeridae)	Visible area of ornamentation	26.60	11.78	0.000	1
Passer domesticus (Aves, Passeridae)	Hue (ornamentation)	13.80	4.95	0.000	1
Pavo cristatus (Aves, Phasianidae)	Train length	23.90	10.34	0.000	7
Pavo cristatus (Aves, Phasianidae)	No. of ocelli	84.00	42.39	0.000	7
Pavo cristatus (Aves, Phasianidae)	Diameter of ocelli	27.50	12.26	0.000	7
Thalassoma bifasciatum (Perciformes, Labridae)	Black + white area	26.55	11.75	0.000	11
Thalassoma bifasciatum (Perciformes, Labridae)	White area	32.87	15.12	0.000	11
Thalassoma bifasciatum (Perciformes, Labridae)	Tail length	23.33	10.03	0.000	11
Tyrannus forficatus (Aves, Tyrannidae)	Tail length (male)	13.60	4.84	0.000	9
Tyrannus forficatus (Aves, Tyrannidae)	Tail length (female)	14.00	5.06	0.000	9