

Does a trade-off exist between sexual ornamentation and ecological plasticity? Sexual dichromatism and occupied elevational range in finches

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Secondary sexual traits are thought to be costly to produce and maintain, and the allocation of energy to sexual traits could result in reduced investment in traits associated with growth and basic maintenance. It has been suggested that the trade-off between sexual traits and growth and maintenance traits should manifest itself in the correlation between development of sexual traits and resistance to environmental variability. Interspecifically, this hypothesis predicts that species with greater sexual ornamentation and dimorphism should be able to tolerate a narrower width of environmental condition compared to related species with less developed sexual traits. We tested this prediction by examining whether sexual dimorphism in cardueline finches was negatively associated with the width of elevational range occupied during breeding. We assumed that the range in elevations where breeding can occur represents a measure of tolerance of environmental variability. We found a positive rather than a negative relationship between breeding range and sexual dimorphism. Finches that were capable of breeding over a large range of elevations were also more dimorphic in plumage. Possible explanations for the observed relationship between sexual dichromatism and ecological breadth could include interspecific differences in food availability and foraging ability, as well as variation in energy required for baseline metabolism.

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Resource allocation to the development and maintenance of secondary sexual traits is often viewed as an energetically costly undertaking, and these traits may serve as reliable indicators of individual quality (reviewed in Andersson 1982, 1994, Hill 1995a). Hence, it is assumed that the phenotypic expression of sexual ornaments is ultimately linked to physiological and developmental pathways that allocate an organism's resources between the competing demands of maintenance, growth, and reproduction (Williams 1966, Zahavi 1975, Kodric-Brown and Brown 1984, Zeh and Zeh 1988, McLain 1991, Promislow et al. 1992, Wine-miller 1992, Emlen 1996). Indeed, it was shown that environmental stress from inadequate nutrition (e.g.,

Swaddle and Witter 1994, Badyaev 1998), increased parasite infestation (e.g. Potti and Merino 1996, Salvador et al. 1996), decreased habitat suitability (Manning and Chamberlain 1994), radioactive pollution (Møller 1993), or climatic extremes (e.g. Parsons 1995) may directly influence allocation patterns and the expression of condition-dependent secondary sexual traits. However, while there may be a strong relationship between expression of sexually selected traits and environmental stress at the population level (reviewed in Hill 1995a), the effects of environmental stress on variation in sexual ornamentation *among* species are less clear. For example, it has been suggested that species subject to strong sexual selection may be less ecologically plastic,

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because energy allocated towards sexual ornamentation is unavailable for other traits associated with an organism's ability to track environmental changes (e.g. McLain 1993). In addition, strong local selection that favors location-specific partitioning of resources between sexual ornaments and other traits may limit species dispersal ability and, thus, occupied range (e.g., Kirkpatrick and Barton 1997). Lower ecological plasticity of species under strong sexual selection has been attributed to low competitive and dispersal capabilities, narrow physiological tolerances, and higher vulnerability to predators and parasites (McLain 1993, McLain et al. 1995). For example, higher probability of extinction for sexually-dimorphic versus monomorphic bird species introduced to tropical islands may result from an underlying trade-off between investment in competitive ability and sexual ornamentation (McLain et al. 1995). Yet, to our knowledge, no comparative studies have examined whether the proposed trade-off exists between ecological plasticity and sexual dimorphism.

Here we examine if ability to tolerate a wide range of ecological environments is associated with sexual dichromatism across all extant finches of the subfamily Carduelinae. Cardueline finches (126 species) provide a powerful system in which to examine the trade-off between ecological plasticity and sexual dimorphism because finches vary extensively in plumage dimorphism and occupy a wide variety of environmental conditions, occurring across the largest range of elevations of any extant birds (Clement et al. 1993, Badyaev 1997a, b). Development of sexual traits is closely associated with fecundity and mortality in cardueline finches, suggesting that sexual traits are costly to maintain and produce (Martin and Badyaev 1996, Badyaev 1997c). We assumed that the range of occupied elevations provides a good estimate of tolerance to environmental variability, because wider elevational ranges are commonly associated with greater environmental variability (Agachanyanch 1981, Badyaev 1993). Biogeographical studies suggest that elevational range occupied by finches is mostly limited by tolerance of environmental conditions during breeding season (Boehme 1975, Badyaev 1987). Therefore, range of elevations occupied during breeding provides a particularly good estimate of environmental variability for our study. Sexual dichromatism often has been used as a measure of the intensity of sexual selection in interspecific studies (e.g., Hamilton and Zuk 1982). Using variation in sexual dimorphism as an indirect measure of the intensity of sexual selection, we specifically tested whether tolerance to environmental variability is associated with a species' ability to invest in sexual ornamentation, e.g., whether sexual dimorphism is negatively correlated with the range of elevations occupied by a species. Developmental control of sexually-selected traits is often more relaxed compared to non-sexual traits (e.g. Møller and Pomiankowski 1993, Parsons

1995) and therefore sexual traits should be more responsive to variation in environmental conditions. Thus, we also compared variation in sexually-selected and non-sexually selected trait (female wing, Badyaev 1997b) in relation to the range of breeding elevations.

Methods

Range of elevation was calculated as the highest minus the lowest elevation of each species breeding distribution across the entire geographic range (see Appendix A in Badyaev 1997b). Two independent observers scored sexual dichromatism for three body regions (rump, breast, and head) from illustrations of males and females in Clement et al. (1993). Dichromatism was recorded for each body region as 0 if there was little or no dichromatism, 1 for moderate dichromatism, and 2 for high dichromatism (e.g., Badyaev 1997b). The plumage dichromatism index was then the mean sum of scores for the three regions between the two observers and mean interscorer values were used in analyses (see Badyaev 1997b for data in Appendix A and more details). To examine biases in observers' scoring, sexual dimorphism scores provided by human observers in this study were compared to scores obtained for the same data set by using the Colortron scoring device (Badyaev and Hill unpubl.). There was a close agreement between the observers' and Colortron scoring (Badyaev 1997b, Badyaev and Hill unpubl.). The use of color plates to score plumage dichromatism assumes an accurate depiction of the species' coloration by the artist and then high quality reproduction of the original plates by the publisher. To test the assumption that the color plates in Clement et al. (1993) are a reasonable depiction of cardueline finch coloration, the plumage coloration of a subset of 33 species of cardueline finches (all species available in the Museum of Natural Sciences at Louisiana State University) was measured with the Colortron. Again, there was a very strong concordance between Colortron measurements of study skins, Colortron measurements, and human observer scores taken from plates in Clement et al. (1993) (Badyaev and Hill, unpubl.). Log (female weight) was used as a measure of body size. In addition to sexually selected traits we examine variation in a non-sexual trait – female wing length (residuals from regression of female wing length on female body mass) in relation to range of elevations (see Table 1 in Badyaev 1997a and Appendix A in Badyaev 1997b)

The phylogeny of cardueline finches represents a consensus tree constructed by summarizing all recent systematics data available for each clade and is described in detail elsewhere (Badyaev 1997b). We did not have consistent estimates of branch lengths because

data came from studies using different methods. All extant cardueline species were included in the phylogenetic tree, and plots of standardized contrasts against the variances of the untransformed contrasts showed no significant correlation. Therefore, the statistical use of equal branch lengths is justified (Garland et al. 1992, Purvis and Rambaut 1995). To control for species relatedness, we calculated independent contrasts between tips and nodes of the tree for the traits of interest (Felsenstein 1985) and examined the relationships between range of elevations and sexual dichromatism by calculating linear through-the-origin regressions on these contrasts (Garland et al. 1992, Purvis and Rambaut 1995). We also analyzed data using pairwise comparisons, where pairs of closely related congeners (Table 2 in Badyaev 1997a) were ranked by the range of breeding elevations and then compared with respect to dichromatism. Concordance with predictions was then tested with a sign test.

Both elevation of breeding and body size correlate with sexual dichromatism in cardueline finches. Smaller or low-elevation species show greater dichromatism than larger or high-elevation species (Björklund 1990, Badyaev 1997b). Therefore, we included maximum elevation and body size into regression analyses to statistically control for their effects on variation in sexual dimorphism.

Results

We had data on both elevational range and sexual dichromatism for 23 pairs of closely related species; in 18 (78%) of these pairs, species with a greater range of elevations were more sexually dimorphic (sign test, $p = 0.0002$). Range of elevations was not associated with wing length ($k = 9$, $n = 20$; sign test, $p = 0.8$).

Degree of sexual dichromatism was positively correlated with range of breeding elevations (Spearman $r = 0.32$, one-tailed $t = 2.21$, $p = 0.03$; Fig. 1A). This trend remained when effects of maximum elevation and body size were statistically controlled ($b_{ST} = 0.22$, $t = 1.8$, $p = 0.04$; Fig. 1B). Wing length did not correlate with range of elevations (Spearman $r = 0.01$, $t = 0.27$, $p = 0.79$; Fig. 2A). The relationship remained non-significant when effects of maximum elevation were statistically controlled ($b_{ST} = 0.024$, $t = 0.21$, $p = 0.83$; Fig. 2B).

Discussion

Sexual selection may lower population fitness, because investment in sexual ornaments can reduce resource allocation to other traits associated with individual fitness, thus limiting the response to natural selection

(Lande 1980, Arnold and Wade 1984, McLain 1993). It has been suggested that across species a similar set of trade-offs might cause negative association between development of sexual traits and tolerance of environmental variability (McLain 1993, McLain et al. 1995). In this study we found that opposite to the latter prediction, sexual dimorphism in cardueline finches was positively associated with a species' ability to tolerate environmental variability. Specifically, as the range between highest and lowest breeding elevation increased, so did species' sexual dimorphism in plumage (Fig. 1). Thus, our results did not support the a priori prediction that a negative relationship should exist across species between ecological plasticity and sexual dimorphism (e.g. McLain 1993, McLain et al. 1995). On the contrary, it appears that finches capable of occupying a wide range of environmental conditions are also able to invest more in sexual ornamentation compared to related species with reduced environmental tolerance (Fig. 1). Furthermore, a non-sexually selected trait (female wing length) did not vary with range of elevations

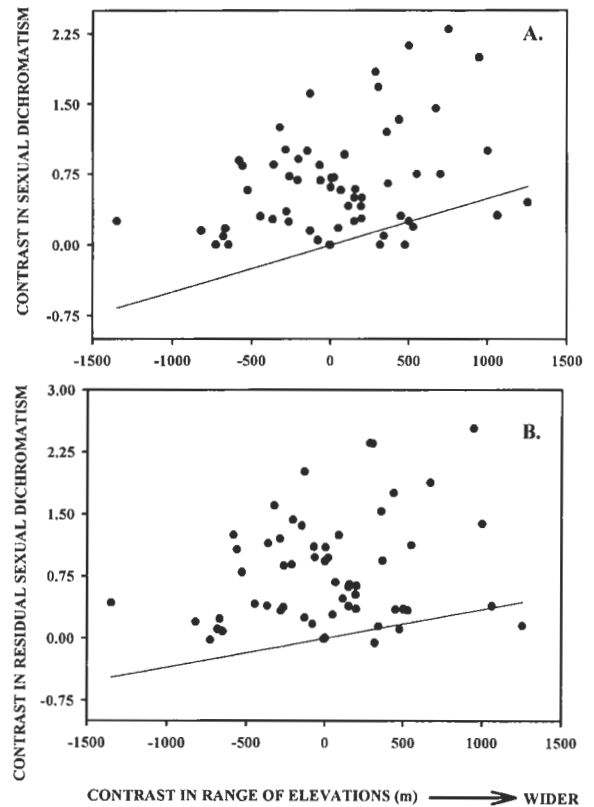


Fig. 1. Regression plots of data transformed by the method of independent contrasts (which controls for possible phylogenetic effects) illustrating the relationship between range of elevations occupied during breeding and (A) sexual dichromatism (Spearman $r = 0.32$, $t = 2.21$, $p = 0.03$), and (B) the standardized residuals of sexual dichromatism corrected for maximum elevation and body size ($b_{ST} = 0.22$, $t = 1.8$, $p = 0.04$).

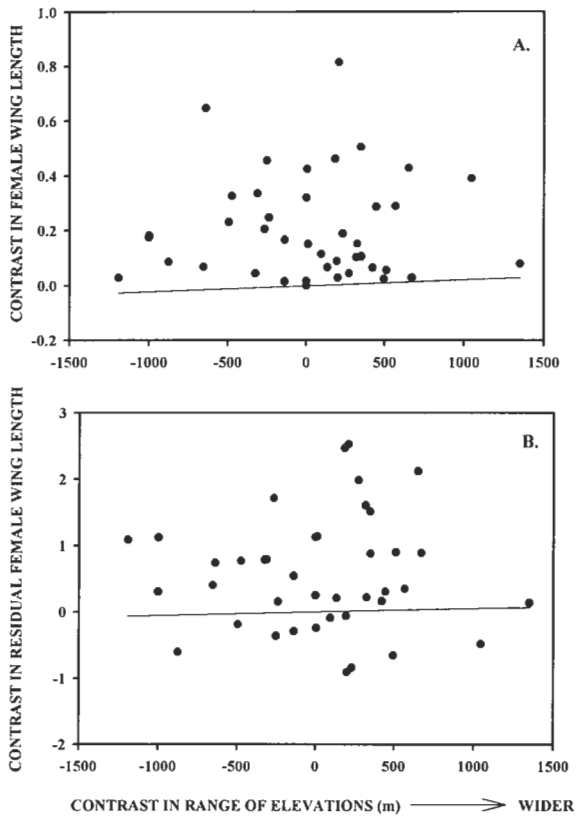


Fig. 2. Regression plots of data transformed by the method of independent contrasts (which controls for possible phylogenetic effects) illustrating the relationship between range of elevations occupied during breeding and (A) female wing length (Spearman $r = 0.01$, $t = 0.27$, $p = 0.79$), and (B) the standardized residuals of female wing length corrected for maximum elevation ($b_{ST} = 0.024$, $t = 0.21$, $p = 0.83$).

(Fig. 2), suggesting that the relationship between environmental variability and variation in sexually and non-sexually selected traits may have different underlying rules of resource and energy allocation and different developmental control (e.g. Møller and Pomiankowski 1993).

Assuming that the range of breeding elevations is a valid measure of a species' ability to tolerate environmental variability, there may be multiple pathways in which sexual dichromatism in finches may be related to the range of breeding elevations. McLain (1993) assumed that species are constrained in their ability to adapt to environmental changes because finite resources cannot simultaneously be allocated to competing demands (e.g. Levins 1968, Sibly and Calow 1986). However, because even closely related species may drastically differ in baseline energy expenditure (Gavrilov 1995), and in ability to acquire resources (Karasov 1990, Diamond and Hammond 1992), there may be no a priori reason to expect a similar trade-off across species. We suggest two potential alternative

mechanisms for why we observed a positive rather than a negative relationship between sexual dimorphism and ability to tolerate environmental variation. First, a trade-off between investment in sexual ornaments and ecological breadth may indeed exist as suggested (McLain 1993, McLain et al. 1995); however, finches capable of breeding over a wider range of elevations may be better at acquiring resources, either because they have greater food availability or are inherently more efficient foragers (Karasov 1990). If this is the case, then the underlying trade-off between competing demands will be masked at the phenotypic level because acquisition of resources differs among species (van Noordwijk and de Jong 1986). This explanation is corroborated by the observation that most of the interspecific variation in sexual dichromatism in cardueline finches is due to changes in diet-dependent carotenoid-based plumage coloration, and carotenoid-based coloration also contributes the most to overall dichromatism (Badyaev and Hill unpubl.). The capacity to produce carotenoid-based coloration is directly linked to ability to acquire carotenoids from food (e.g. Brush 1990) and that ability may vary both within and among species (e.g. Hill 1995b). It is therefore possible that finch species that occupy wider range of elevations may be better at acquiring carotenoid-rich foods. It is interesting to mention that McLain et al. (1995) found no association between plumage coloration and risk of extinction in fringillid finches, while the relationship was pronounced in other families. Studies of foraging efficiency between sexually dimorphic and monomorphic species may provide some insight into this hypothesis.

Alternatively, species with a broad tolerance to environmental variance may have low energy expenditure for basal metabolism (Zotin 1990, Hoffmann and Watson 1993, Djawdan et al. 1997), such that metabolic energy not used in maintenance and survival is available for sexual selection to act on, resulting in morphological evolution (Sibly and Calow 1986, Koehn and Bayne 1989, Hoffmann and Parsons 1991, Kieser 1993, Parsons 1993a, b). Living fossils are often cited as an extreme example, where little evolutionary change can occur when the cost of accommodating environmental stress is high (Parsons 1993a, b). Under this scenario, sexually dimorphic finches capable of breeding over a wide range of elevations are expected to expend less energy on maintenance and survival costs than the more ecologically restricted monomorphic species (e.g. Parsons 1995). Empirical studies of the energy budgets of species occupying broad and narrow elevational ranges are needed to test whether differences exist in metabolic costs across a range of temperatures, and whether there are differences in acclimation ability across species. If species actually differ physiologically, then each species should have a unique set of trade-offs and it would be invalid to assume that sexual dimor-

phism should always negatively correlate with tolerance to environmental variability.

Ecological condition associated with elevation strongly affects paternal investment and intensity of sexual selection in finches (Badyaev 1997c). Similarly, the intensity of sexual competition may vary with environmental stress resulting in more variable selection intensity in widely fluctuating environments.

In sum, although it has been suggested that investment in sexually-selected traits and greater sexual dimorphism may result in reduced ecological plasticity, we found a positive rather than a negative relationship between sexual dichromatism and elevational range occupied by cardueline finches. Yet, without a better understanding of the underlying processes that determine trade-offs across species it is difficult to know which predictions should be expected. Comparative field studies of ecologically similar species that differ in the intensity of sexual selection should provide greater insight into the critical predictions that need testing.

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References

Agachanyanch, O. E. 1981. Mountain environment and geographical models of flora formation. – Misl, Moscow.

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

Andersson, M. 1994. Sexual selection. – Princeton Univ. Press, Princeton, NJ.

Arnold, S. J. and Wade, M. J. 1984. On the measurement of natural and sexual selection: theory. – *Evolution* 38: 709–719.

Badyaev, A. V. 1987. Composition and distribution of the Pamir-Alay Mountain avifauna (98 spp.) and peculiarities of avian biology in conditions of subalpine juniper bush belt. Thesis, Moscow Univ., Moscow.

Badyaev, A. V. 1993. Breeding biology of the gold-fronted serin (*Serinus pusillus*) in conditions of subalpine bush zone of the Phansky Mountains. – *Biol. Sciences (Biol. Nauk.)* 348: 89–99.

Badyaev, A. V. 1997a. Avian life history variation along altitudinal gradients: an example with Cardueline finches. – *Oecologia* 111: 357–364.

Badyaev, A. V. 1997b. Altitudinal variation in sexual dimorphism: a new pattern and alternative hypotheses. – *Behav. Ecol.* 8: 675–690.

Badyaev, A. V. 1997c. Covariation between sexually selected and life history traits: an example with Cardueline finches. *Oikos* 80: 128–139.

Badyaev, A. V. 1998. Environmental stress and developmental stability in dentition of the Yellowstone grizzly bears. *Behav. Ecol.* 9: 277–282.

Björklund, M. 1990. A phylogenetic interpretation of sexual dimorphism in body size and ornament in relation to mating system in birds. – *J. Evol. Biol.* 3: 171–183.

Boehme, R. L. 1975. Birds of the South Palearctic Mountains. Moscow Univ. Press, Moscow.

Brush, A. H. 1990. Metabolism of carotenoid pigments in birds. *FASEB J.* 4: 2969–2977.

Clement, P., Harris, A. and Davis, J. 1993. Finches and sparrows: an identification guide. Princeton Univ. Press, Princeton, NJ.

Diamond, J. M. and Hammond, K. A. 1992. The matches, achieved by natural selection between biological capacities and their natural loads. *Experientia* 48: 551–557.

Djawan, M., Rose, M. L. and Bradley, T. J. 1997. Does selection for stress resistance lower metabolic rate? *Ecology* 78: 828–837.

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

Felsenstein, J. 1985. Phylogenies and the comparative method. – *Am. Nat.* 125: 1–15.

Hamilton, W. D. and Zuk, M. 1982. Heritable true fitness and bright birds: a role for parasites? – *Science* 218: 384–387.

Hill, G. E. 1995a. Ornamental traits as indicators of environmental health. *BioScience* 45: 25–31.

Hill, G. E. 1995b. Interspecific variation in plasma hue in relation to carotenoid plumage pigmentation. *Auk* 112: 1054–1057.

Hoffmann, A. A. and Parsons, P. A. 1991. Evolutionary genetics and environmental stress. – Oxford Univ. Press, Oxford.

Hoffmann, A. A. and Watson, M. 1993. Geographical variation in the acclimation responses of *Drosophila* to temperature extremes. – *Am. Nat.* 142: S93–S113.

Garland, T. Jr., Harvey, P. H. and Ives, A. R. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. – *Syst. Biol.* 41: 18–32.

Gavrilov, V. M. 1995. Quantitative interrelations between food consumption, energetic metabolism, environmental temperature and body mass in Family Corvidae. – *Ornitologia* 165–173.

Karasov, W. H. 1990. Digestion in birds: chemical and physiological determinants and ecological implications. *Stud. Avian Biol.* 13: 391–415.

Kieser, J. A. 1993. Evolution developmental instability and the theory of acquisition. *Genetica* 89: 219–225.

Kirkpatrick, M. and Barton, N. H. 1997. Evolution of a species' range. – *Am. Nat.* 150: 1–23.

Kodric-Brown, A. and Brown, J. H. 1984. Truth in advertising: the kinds of traits favored by sexual selection. – *Am. Nat.* 124: 309–323.

Koehn, R. K. and Bayne, B. L. 1989. Towards a physiological and genetical understanding of the energetics of the stress response. – *Biol. J. Linn. Soc.* 37: 157–171.

Lande, R. 1980. Sexual dimorphism, sexual selection and adaptation in polygenic characters. – *Evolution* 34: 292–307.

Levins, R. 1968. Evolution in a changing environment. Princeton Univ. Press, Princeton, NJ.

Manning, J. T. and Chamberlain, A. T. 1994. Fluctuating asymmetry in gorilla canines: a sensitive indicator of environmental stress. *Proc. R. Soc. Lond. B* 255: 189–193.

Martin, T. E. and Badyaev, A. V. 1996. Sexual dichromatism relative to nest height and nest predation: contributions of females versus males. – *Evolution* 50: 2454–2460.

McLain, D. K. 1991. The r-K continuum and the relative effectiveness of sexual selection. – *Oikos* 60: 263–265.

McLain, D. K. 1993. Cope's rules, sexual selection and the loss of ecological plasticity. *Oikos* 68: 490–500.

- McLain, D. K., Moulton, M. P. and Redfearn, T. P. 1995. Sexual selection and the risk of extinction of introduced birds on oceanic islands. – *Oikos* 74: 27–34.
- Møller, A. P. 1993. Morphology and sexual selection in the barn swallow *Hirundo rustica* in Chernobyl Ukraine. – *Proc. R. Soc. Lond. B* 252: 51–57.
- Møller, A. P. and Pomiankowski, A. 1993. Fluctuating asymmetry and sexual selection. – *Genetica* 89: 267–279.
- Parsons, P. A. 1993a. The importance and consequences of stress in living and fossil populations: from life-history variation to evolutionary change. – *Am. Nat.* 142: S5–S20.
- Parsons, P. A. 1993b. Developmental variability and the limits of adaptation: interactions with stress. – *Genetica* 89: 245–253.
- Parsons, P. A. 1995. Stress and limits to adaptation: sexual ornaments. – *J. Evol. Biol.* 8: 455–461.
- Potti, J. and Merino, S. 1996. Parasites and the ontogeny of sexual size dimorphism in a passerine bird. – *Proc. R. Soc. Lond. B* 263: 9–12.
- Promislow, D. E. L., Montgomerie, R. D. and Martin, T. E. 1992. Mortality costs of sexual dimorphism in birds. – *Proc. R. Soc. Lond. B* 250: 143–150.
- Purvis, A. and Rambaut, A. 1995. Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analyzing comparative data. *Comp. Appl. Biosci.* 11: 247–251.
- Salvator, A., Veiga, J. P., Martin, J., Lopez, P., Abekenda, M. and Puerta, M. 1996. The cost of producing a sexual signal: testosterone increases the susceptibility of male lizards to ectoparasitic infestation. – *Behav. Ecol.* 7: 145–150.
- Sibly, R. M. and Calow, P. 1986. *Physiological ecology of animals: an evolutionary approach.* – Blackwell Scientific, Oxford.
- Swaddle, J. P. and Witter, M. S. 1994. Food feathers and fluctuating asymmetry. – *Proc. R. Soc. Lond. B* 255: 147–152.
- van Noordwijk, A. J. and de Jong, G. 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. – *Am. Nat.* 128: 137–142.
- Williams, G. C. 1966. *Adaptation and natural selection.* Princeton Univ. Press, Princeton, NJ.
- Winemiller, K. O. 1992. Life-history strategies and the effectiveness of sexual selection. – *Oikos* 63: 318–327.
- Zahavi, M. 1975. Mate selection – a selection for a handicap. – *J. Theor. Biol.* 53: 205–214.
- Zeh, D. H. and Zeh, J. A. 1988. Condition-dependent sex ornaments and field tests of sexual-selection theory. – *Am. Nat.* 132: 454–459.
- Zotkin, A. I. 1990. *Thermodynamic bases of biological processes: physiological reactions and adaptations.* – De Gruyter, Berlin.