Rensch's Rule in *Dichroplus pratensis*: A Reply to Wolak

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The critique of our paper (Bidau and Martí 2007) by Wolak (2008) is based on two premises: 1) a misinterpretation of Rensch's rule definition and 2) the statistical methodology. Regarding point 1, we do not agree. Rensch (1950) described an interspecific pattern by which, in phylogenetically related species (he used as examples, mammals, birds, and carabid beetles), sexual size dimorphism (SSD) increases with the increase of general body size: ". . . the rule is valid that in numerous animal groups the sexual dimorphism increases with body size" (Webb and Freckleton 2007, also see Reiss 1989, p. 117). Also, in a review of contemporary bird literature (Anonymous 1951) the following commentary was made on the paper by Rensch (1950): "Animals of large size show relatively greater sexual dimorphism than do closely related animals of smaller size."

Interestingly, this criterion is still used in many recent papers on SSD (see below). Later, Rensch (1959) stated that "In species of birds in which the male is larger than the female, the relative sexual difference [in size] increases with body size. If by way of exception, the females are larger than the males, as among many species of birds of prey, the opposite correlation applies, i.e., the greater sexual difference is found in the smaller species, as cited by Wolak (2008) and Selander (1966). Rensch (1959) was probably speaking of an "exception" because, although cases of female-biased SSD were already known, he thought that "reversed" SSD was a totally different phenomenon (see below). Although no evidence of the former is provided by Rensch (1959) and in a 1953 reference (cited in Rensch, 1959 and Reiss, 1989, p. 170), many studies have analyzed SSD in relation to Rensch's rule in insects and other taxa where females are larger than males. Again, results are conflicting and not conforming to a general "rule" (Webb and Freckleton 2007).

Wolak (2008) states that "Rensch's Rule is fully defined as the allometry observed when SSD increases with size if males are the larger sex, but when SSD decreases with size if females are the larger sex." This is not Rensch's truly original definition but that of Fairbairn (1990, 1997) and Fairbairn and Preziosi (1994). In fact, some recent papers use the original definition of Rensch's rule. For example, Dale et al. (2007, p. 2971) say, "In 1950, Rensch first described that in groups of related species, sexual size dimorphism is more pronounced in larger species. This widespread and fundamental allometric relationship is now commonly referred as 'Rensch's rule.'" Furthermore, although Rensch's first proposal, the increase of SSD in cases of male-biased SSD (MBSSD), has received wide support, the decrease of SSD when the female is the larger sex (FBSSD) remains unproved (Webb and Freckleton 2007), even in birds of prey, Rensch's (1959) original example (Webb and Freckleton 2007, table 2).

Other problems of definition occur: in a recent paper (Blanckenhorn et al., 2007, p. 246) state that, "Rensch (1950) observed that SSD increases with body size in species where males are larger and decreases with body size in species where females are larger (recently termed Rensch's rule; Abouheif and Fairbairn 1997; Fairbairn 1997)." The former is not exactly correct: literature on SSD mentions the pattern which is being discussed in this paper as Rensch's rule, at least since 1966. See, for example, the discussion of Selander (1966) discussion under "Body Size and Sexual Dimorphism," p. 142–143. Also, Earhart and Johnson (1970), p. 255, in their study of owls, observe that, "This increased dimorphism in the larger species contradicts "Rensch's Rule", and Gibbons and Lovich (1990), p. 10, in a work on sexual dimorphism of turtles, indicate that "The absence of an obvious relationship casts serious doubts on the applicability of 'Rensch's Rule', . . . ".

In our paper, we tried to establish whether Rensch's rule operated at an intraspecific level in the grasshopper *Dichroplus pratensis* Bruner. Intraspecific evidence of Rensch's rule in most animals is very scarce (Bidau and Martí 2007, 2008). We analyzed the patterns of SSD in a species showing high body size variation related to geographic factors. We chose to use the classical Rensch's rule definition as considered above, because exceptions to Rensch's rule sensu Fairbairn and Preziosi (1994), are very numerous (Webb and Freckleton 2007). Independently of the allometric trend that theoretically seems to be the same as shown by Fairbairn (1997), factors responsible for SSD in species with FBSSD, are probably a response to totally different evolutionary constraints. In fact, trends are not mechanisms neither processes. Furthermore, our approach to SSD in *D. pratensis* was obviously intraspecific. Intraspecific Rensch's rule has no confirmation whatsoever due to the lack of a reasonable number of proper studies (see Blanckenhorn et al. (2007)).

Regarding the second point raised by Wolak (2008), we do agree that type II regression is the best approach to analyze SSD (Ranta et al. 1994; Fairbairn 1997). Our data were reanalyzed using reduced major axis regression (Bidau and Martí 2008); although the result was different from that reported originally (Bidau and

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Martí 2007), the regression slope was nevertheless significantly <1 ($\beta = 0.7217$). Again, according to the extended definition of Rensch's rule, Wolak (2008) is right. According to the conservative definition we used and that is discussed here, Rensch's rule is inverted. However, our results are validated independently of the definition used, a definition that, as demonstrated, is far from being clear.

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