

A brachypterous butterfly?

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Butterflies of the genus *Redonda* Adams & Bernard (Lepidoptera: Nymphalidae: Satyrinae) are endemic to the Andes of Venezuela. They comprise a monophyletic group of five allopatric taxa, females of which show various degrees of wing reduction and ability to fly. The female of *Redonda bordoni* Viloría & Pyrcz sp. nov. appears to be brachypterous and incapable of sustained flight, a phenomenon previously unknown within the Rhopalocera.

Keywords: flightlessness; Lepidoptera; Nymphalidae; *Redonda*; Satyrinae; Venezuela

1. INTRODUCTION

Brachyptery, or wing reduction coupled with flightlessness, although hitherto unknown in butterflies (Rhopalocera), has evolved independently several times in moths (Heterocera). This phenomenon, which is almost entirely restricted to females, occurs in at least 26 of the 120 plus currently recognized families (Heppner 1991; Sattler 1991; Sattler & Wojtusiak 1999).

Brachyptery may be less likely to evolve in butterflies because not only do female butterflies need to be able to fly to search for nutrient sources and larval host plants, but they actively participate in mate location and/or courtship (Silberglied 1984).

2. METHODS

The research presented here is based on 7 years (1993–2000) of extensive collecting and observation of butterflies of the genus *Redonda* Adams & Bernard (figure 1) in the Venezuelan Andes. Specimens of *Redonda bordoni* sp. nov. were studied and collected in the Páramos del Batallón and La Negra (Táchira State) during five periods of 3 to 10 days, from February 1994 to March 2000. All individuals collected are included in the morphometric analysis discussed below, but only specimens collected before 2000 were used for taxonomic work. Digital images of the butterflies were analysed with NIH IMAGE v. 1.6 and IMAGEJ v. 1.25 to calculate wing length and area.

To rule out artefacts caused by the small sample size of females, the null hypothesis that male and female samples were drawn from the same pool of specimens was tested using smoothed bootstrap techniques. An empirical probability density function was estimated from the data. From this function 1000 random samples of sizes m and f were taken, and the differences in the median of both bootstrapped samples $\Delta^* = M_m^* - M_f^*$ were computed and compared with the differences between the real values $\Delta = M_m - M_f$.

(a) Analysis of wing size and shape

The ratio of female-to-male forewing length can be used to compare the degree of sexual dimorphism in butterfly species (figure 2), but in cases of wing reduction this ratio might not reflect the actual degree of difference (Sattler 1991). Differences in wing area between species, and between sexes within each species are presented instead.

Differences in area alone do not necessarily mean that there is wing reduction, because this could be due to differences in body size and the consequent scaling of other organs, which follows the equation: $\log y = \beta_0 + \beta_1 \log m$, where m is the body mass, β_0 and β_1 are constants, and y is the scaled organ. Thus, as wing area scales to body size with a ratio of $\beta_1 = 2/3$ (area to volume), wing length scales with a factor of $\beta_1 = 1/3$ (length to volume) (Wickman & Karlsson 1989). A departure from this trend is found in lepidopteran species with tendencies towards wing reduction: female wings seem to be more slender and wing venation looks deformed, although it might not be reduced (Sattler 1991). Wing shape can be assessed using the aspect ratio (λ) (Brodsky 1994), which is given by the squared wing span s divided by wing area a : $\lambda = s^2/a$, (Wickman 1992). Slender wings have higher aspect ratios than broad wings. Under the null hypothesis that wing reduction in females is due to scaling of organs, the aspect ratio of the wing should be the same as for males. To test this, the aspect ratio function was calculated from a linear regression of wing area a over squared wing span s^2 for males of *R. bordoni* sp. nov. This function is used to predict the wing area of female specimens given their wing span; predicted and observed values are then compared.

3. RESULTS AND DISCUSSION

Three species and two subspecies of *Redonda* (figure 1) occur allopatrically in five páramos (high altitude Andean grassland) along the Andes of Venezuela. Males of all taxa have well-developed wings and are strong flyers, but females show a geographical cline of progressive reduction in flight ability and wing size, the latter resulting in an increasing degree of sexual dimorphism in wing surface area (figure 3). Sexual differences in the median of wing area within each species are significantly different from random samples ($p_{\Delta < \Delta^*} < 0.01$). Except for the northernmost species, male and female wing areas do not overlap. Wing reduction in the female is most pronounced in the species hereby diagnosed (a description is given in electronic Appendix A, available on The Royal Society's Publications Web site).

(a) *Redonda bordoni* Viloría & Pyrcz sp. nov.

(i) Diagnosis

Antennal club broad, concave, ventromesial surface with three longitudinal carinae (family: Nymphalidae). Base of forewing subcosta (Sc) notably swollen (subfamily: Satyrinae). Eyes hairy. Palpi twice as long as head. Forewing venation: Sc, first and second radial branches all independent; root of third radial branch closer to root of fourth radial branch than to discal cell; no radial-median cross-vein; first median cross-vein (m1–m2) strongly curved inwards. Hindwing venation: humeral vein developed; m1–m2 curved inwards; discal cell longer than half wing length (tribe: Pronophilini). Hindwings rounded, without scalloped borders. Female much smaller than male. Male genitalia: subunci absent (genus: *Redonda*); uncus straight, arising at same level as tegumen; valvae subtriangular, without visible processes; aedeagus slightly sinuous, as long as tegumen + uncus; saccus half the size of that of *R. empetrus*. Female genitalia: spermatheca half the size of that of *R. empetrus*, bearing a lagena (absent in other species of *Redonda*); collateral glands globular, intermediate size between those of *R. empetrus* and other species of the genus. Distinctive characters of wing pattern: male forewing, dorsal, without white marks in basal half; female forewing, dorsal, silvery white; hindwing, ventral, of both sexes brown (not

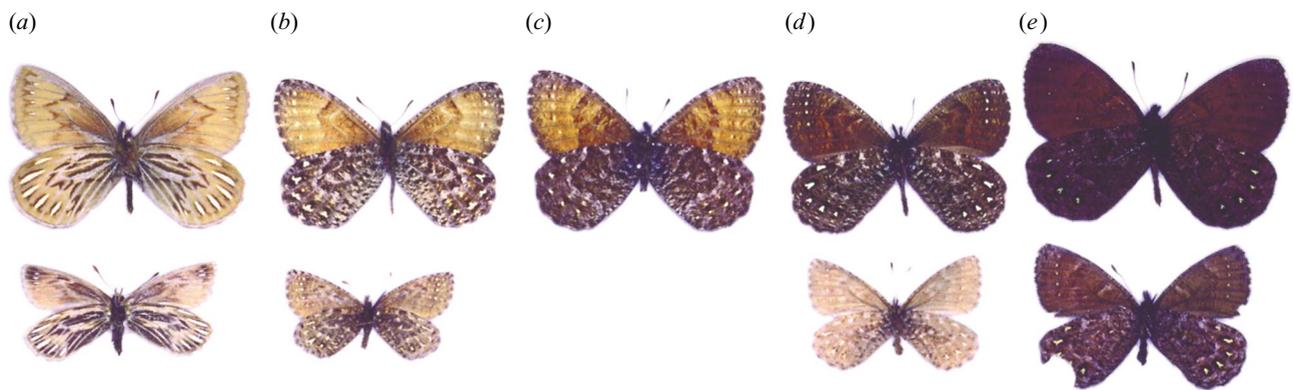


Figure 1. Species and subspecies of *Redonda* (ventral surfaces). (a) *Redonda bordoni* Vioria & Pyrcz sp. nov. male holotype and female allotype; (b) *R. empetrus empetrus* (Thieme); (c) *R. empetrus bolivari* Adams & Bernard (female unknown); (d) *R. empetrus* ssp. nov.; and (e) *Redonda* sp. nov. Top, males; bottom, females.

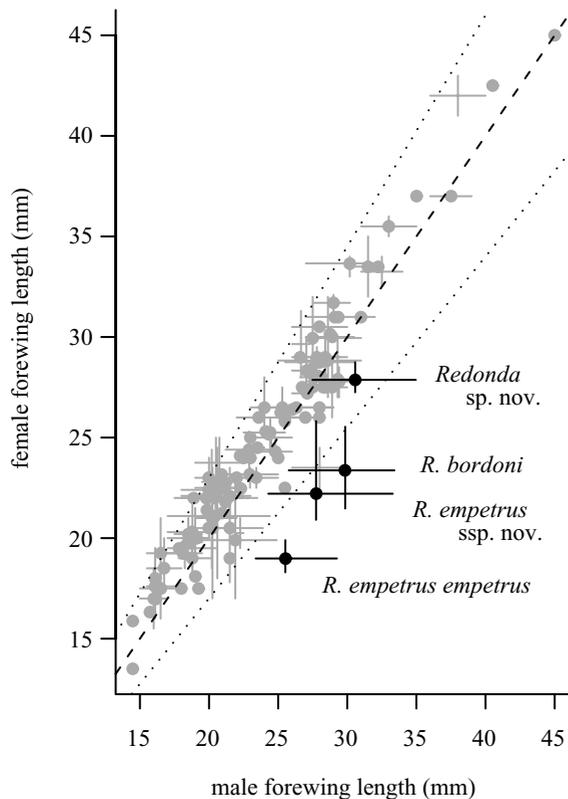


Figure 2. Female versus male forewing length of 131 satyrine taxa from the Americas, Europe, Asia and Oceania (data sources listed in electronic Appendix B). Median values, where available, represented as dots; variation, where available, shown as bars ranging from minimum to maximum values for each sex. The dashed line represents the 1 : 1 female-to-male relationship; almost all species show dimorphism between 0.85 and 1.15 (lower and upper dotted lines). Two *Redonda* species (in black) are below these limits.

marbled), postdiscal series of fusiform white spots, veins continuously covered by white scales.

(ii) *Wing reduction*

The difference in median, $\Delta = 356.76 \text{ mm}^2$, between the sexes of *R. bordoni* was found to be significantly different from differences between random samples ($p_{\Delta < \Delta^*} < 0.001$). This difference cannot be explained by simple organ sca-

ling; the observed values for the females are lower than the predicted values in figure 4, this deviation being significant at the 95% prediction tolerance level.

The wings of female *R. bordoni* are considerably reduced and deformed, which results in abnormal venation (see figure 6c in electronic Appendix A). The five females found during fieldwork were all highly sedentary and were not observed flying; even when we tried to disturb them their reaction was simply to walk further up the grass stems on which they were perching. When one of these individuals was picked up and dropped, it fluttered weakly for a short distance before landing and it appeared incapable of sustained flight. Another female that we kept alive for observation for 3 days in a net cage, made no attempt to fly. The sedentary behaviour of the female combined with its cryptic underside makes it difficult to detect and may be the reason why we observed approximately 30 times as many males as females, despite searching selectively for the latter sex.

In contrast to the females, male *R. bordoni* are energetic flyers and stay on the wing in both sunny and overcast weather. The marked differences in morphology and behaviour between the sexes suggest that males patrol in search of the cryptic females, which are only apparent when displaying the silvery uppersides of their wings.

Páramo weather conditions are extreme, with strong winds, low daily temperatures (annual mean at 3000 m of 10°C), high radiation and frequent cloud immersion. In addition, the páramo of El Batallón is one of the coldest in Venezuela. Its seasonal rainfall pattern is atypical, as the rainy season lasts as long as 10 months (Sarmiento 1986). Flight in this environment would be energetically costly, and might also explain the occurrence of male brachyptery in an endemic, diurnal notodontid moth, *Xenomigia brachyptera* Sattler & Wojtusiak (1999).

Female cloud forest pronophilines lay eggs singly on leaf tips of tall bamboos (DeVries 1987). By contrast, all three species of *Redonda* scatter their eggs, either while crawling (*R. bordoni*) or flying (the other two species) over their páramo habitat (Ferrer-Paris 2000). This oviposition strategy, also recorded for high Andean non-pronophilines (Vioria 1994), and some Palearctic species of *Melanargia* Meigen, *Aphantopus* Wallengren, and *Erebia* Dalman (Schweiserischer Bund für Naturschutz 1987), is only feasible when the host plant is abundant and there is

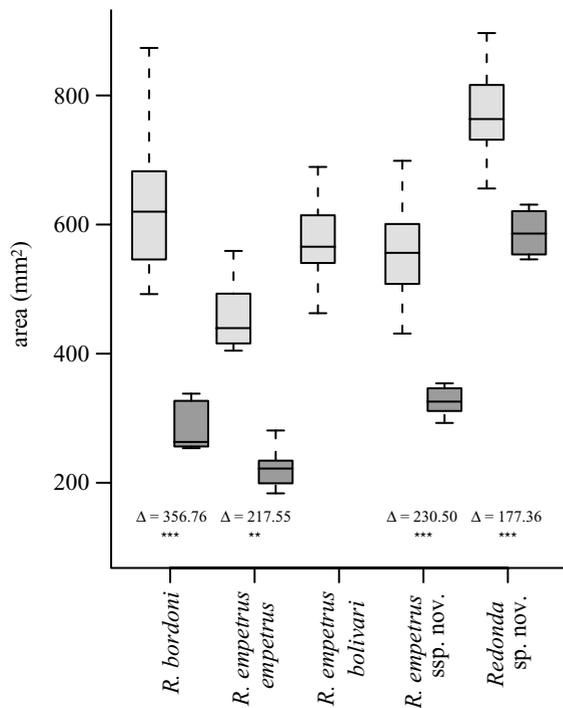


Figure 3. Box-and-whisker plots of the surface area of fore- and hindwings for males (light grey) and females (dark grey) of *Redonda* species and subspecies. The box expands from the first to the third quartile of the data, enclosing 50% of the data; the middle line represents the median; whiskers expand to the extreme values. Species are ordered from south to north. Sample size for males (m) and females (f) are as follows: *R. bordoni* m = 136, f = 5; *R. empetrus empetrus* m = 34, f = 8; *R. empetrus bolivari* m = 22, f = 0; *R. empetrus ssp. nov.* m = 54, f = 9; *Redonda sp. nov.* m = 24, f = 4. ***when $p_{\Delta < \Delta^*} < 0.001$; **when $p_{\Delta < \Delta^*} < 0.01$.

therefore no need to search for individual isolated hosts. We have found larvae of *R. bordoni* feeding on low tussock grasses (*Calamagrostis* sp.), which are the commonest plants in their habitat. Lack of the need to search for larval hosts may be an important factor favouring the loss of flight ability, as its loss would allow females to allocate more time and energy to the process of egg production, thereby increasing fecundity or fitness (Wiklund & Persson 1983; Roff 1990).

Except for West Indian taxa and species of six exclusively oreale genera, the butterflies of the neotropical tribe Pronophilini are forest dwellers. Their diversity peaks in the Andean cloud forest, as does the diversity of woody bamboos (Clark 1995), which comprise their only recorded natural larval host plants (Viloría 1998). Why so few pronophilines inhabit the Andean páramo is unclear, but it may be due to the very recent formation of this biome, at least in the northernmost Andes (Shapiro 1994). Comparative observations of the phylogeny of selected North Andean satyrines (Viloría 1998) and the geological history of the Venezuelan Andes (see Kroonenberg *et al.* 1990; Schubert & Vivas 1993; Rull 1996) suggest that modern oreale endemics among the pronophilines have a recent origin, and that wing reduction in *Redonda* is an apomorphic character that might have evolved after the end of the Mérida glaciation (less than 11 100 years).

Although incapable of sustained flight, females of the butterfly *Eucheira socialis* Westwood (Pieridae) from

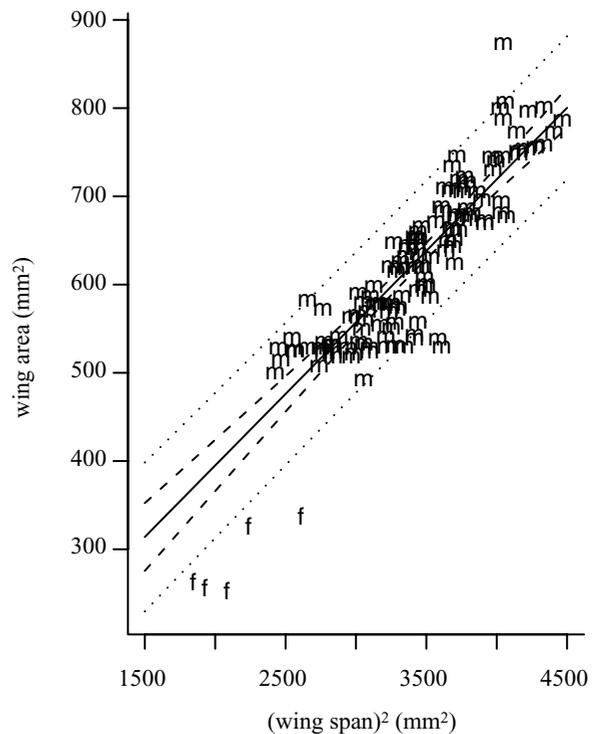


Figure 4. Linear regression of wing area a over the squared wing span s^2 for males of *Redonda bordoni* (m, in the plot). $a = 70.77 \pm 0.16s^2$. Adjusted $R^2 = 0.779$, both intercept and coefficient are significantly different from 0 at the 99% confidence level. The 99% confidence interval of the regression (dashed lines) and the 95% tolerance interval of the prediction (dotted lines) are included. Observed values of females (f) are also shown.

southern Mexico have normally developed wings (although with reduced venation). Poor flight ability in this species is thought to have evolved as a result of its highly unusual population biology and possible anthropogenic selection (Geiger *et al.* 1989).

The evolution of brachyptery in female *R. bordoni* is likely to be partly or wholly due to the three major factors thought to be responsible for the loss of flight in insects: geographical isolation, high energetic cost of flight and habitat stability (Roff 1990; Wagner & Liebherr 1992). However, even though there may be selection for flightlessness in females of this species, the fact that males probably locate them visually is likely to impose constraints on excessive wing reduction.

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Brodsky, A. K. 1994 *The evolution of insect flight*. Oxford University Press.
 Clark, L. G. 1995 Diversity and distribution of the Andean woody bamboos (Poaceae: Bambuseae). In *Biodiversity and conservation of neotropical Montane forests* (ed. S. P. Churchill, H. Balslev, E. Forero & J. Luteyn), pp. 501–512. New York Botanical Garden.
 DeVries, P. J. 1987 *The butterflies of Costa Rica and their natural history: Papilionidae, Pieridae, Nymphalidae*. Princeton University Press.

- Ferrer-Paris, J. R. 2000 The genus *Redonda* (Lepidoptera: Satyrinae): a model to study adaptation and distribution in the páramos of Venezuela. Diplom thesis, Universität Bayreuth, Germany.
- Geiger, H. J., Shapiro, A. M. & Llorente, J. 1989 *Eucheira socialis* Westw. (Pieridae). Loss of genetic variation as a consequence of the population biology and anthropogenic range extension. *Nota Lepid.* **12**, 32.
- Heppner, J. B. 1991 Brachyptery and aptery in Lepidoptera. *Trop. Lepid.* **2**, 11–40.
- Kroonenberg, S. B., Bakker, J. G. M. & Van der Wiel, A. M. 1990 Late Cenozoic uplift and paleogeography of the Colombian Andes: constraints on the development of high-andean biota. *Geol. Mijnbouw* **69**, 279–290.
- Roff, D. A. 1990 The evolution of flightlessness in insects. *Ecol. Monogr.* **60**, 389–421.
- Rull, V. 1996 Late Pleistocene and Holocene climates of Venezuela. *Quaternary Int.* **31**, 85–94.
- Sarmiento, G. 1986 Ecological features of climate in high tropical mountains. In *High altitude tropical biogeography* (ed. F. Vuilleumier & M. Monasterio), pp. 11–45. New York: Oxford University Press.
- Sattler, K. 1991 A review of wing reduction in Lepidoptera. *Bull. Br. Mus. Nat. Hist. Entomol.* **60**, 243–288.
- Sattler, K. & Wojtusiak, J. 1999 A new brachypterous *Xenomigia* species (Lepidoptera: Notodontidae) from Venezuela. *Entomol. Scand.* **30**, 435–442.
- Schubert, C. & Vivas, L. 1993 *El Cuaternario de la Cordillera de Mérida, Andes venezolanos*. Mérida: Universidad de Los Andes/Fundación Polar.
- Schweizerischer Bund für Naturschutz 1987 *Tagfalter und ihre Lebensräume. Arten. Gefährdung. Schutz*. Basel, Switzerland: K. Holliger.
- Shapiro, A. M. 1994 Why are there so few butterflies in the high Andes? *J. Res. Lepid.* **31**, 35–56.
- Silberglied, R. E. 1984 Visual communication and sexual selection among butterflies. *Symp. R. Entomol. Soc. Lond.* **11**, 207–223.
- Viloría, A. L. 1994 High Andean Pronophilini from Venezuela: two new species of *Diaphanos*. *J. Lepid. Soc.* **48**, 180–189.
- Viloría, A. L. 1998 Studies on the systematics and biogeography of some montane satyrid butterflies (Lepidoptera). PhD thesis, University of London/The Natural History Museum, UK.
- Wagner, D. L. & Liebherr, J. K. 1992 Flightlessness in insects. *Trends Ecol. Evol.* **7**, 216–220.
- Wickman, P. O. 1992 Sexual selection and butterfly design: a comparative study. *Evolution* **46**, 1525–1536.
- Wickman, P. O. & Karlsson, B. 1989 Abdomen size, body size and the reproductive effort of insects. *Oikos* **56**, 209–214.
- Wiklund, C. & Persson, A. 1983 Fecundity, and the relation of egg weight variation to offspring fitness in the specked wood butterfly *Pararge aegeria*, or why don't butterfly females lay more eggs? *Oikos* **40**, 53–63.

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