

Tarsal asymmetry, trait size, and extreme phenotypes in a sexually size-dimorphic water boatman *Callicorixa vulnerata*

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Abstract: Fluctuating asymmetry (FA) in morphological traits can vary with the size of characters and the mode of selection acting on them. In a previous study, mid-leg tarsal FA (tarsal spine number and tarsal length) in the water boatman *Callicorixa vulnerata* was inversely related to fitness in both sexes. The mid-legs of water boatmen are used to cling to bottom substrate during underwater feeding and if under stabilizing selection, extreme phenotypes are predicted to exhibit elevated FA. In this study, it is shown that water boatmen with large or small mid-leg tarsal traits tend to have higher levels of tarsal FA than modal phenotypes, possibly because of increased homozygosity, poor genomic balance, or greater stress during development in extreme phenotypes. This relationship suggests selection against asymmetry per se will indirectly impose stabilizing selection on trait size. Regression analyses revealed that the relationship between FA and trait size differed between the sexes and was best described by a U-shaped distribution in females but by a relatively flat, negative linear association in males. These results indicate possible directional selection on male tarsal traits. Alternatively, they suggest associations between FA and trait size do not always reflect the mode of selection acting on a trait.

Résumé : L'asymétrie fluctuante (FA) de caractères morphologiques peut varier selon la taille de ces caractères et le type de sélection qui agit sur eux. Au cours d'une étude antérieure, la FA du tarse de la patte médiane (nombre d'épines tarsales et longueur du tarse) chez la corise *Callicorixa vulnerata* s'est avérée être inversement proportionnelle au fitness chez les deux sexes. Les pattes médianes des corises adhèrent au substrat de fond au cours de l'alimentation sous l'eau et, si le caractère est soumis à une sélection stabilisante, les phénotypes extrêmes devraient avoir des FAs importantes. Dans cette étude, nous démontrons que les corises qui ont des caractères méso-tarsaux grands ou petits sont plus susceptibles d'avoir des FAs tarsales que les phénotypes modaux, peut-être à cause d'une homozygotie importante ou d'un équilibre génomique précaire, ou alors à cause d'un stress plus grand pendant le développement chez les phénotypes extrêmes. Cette relation indique que la sélection à l'encontre de l'asymétrie per se impose indirectement une sélection stabilisante de la taille des caractères. Des analyses de régression révèlent que la relation entre la FA et la taille des caractères est différente chez les mâles et les femelles et c'est une distribution en U qui décrit le mieux cette relation chez les femelles, et une association linéaire négative relativement plate chez les mâles. Ces résultats indiquent probablement qu'une sélection directionnelle agit sur les caractères tarsaux des mâles; ou alors, ils peuvent indiquer que les associations entre la FA et la taille des caractères ne reflètent pas nécessairement le mode de sélection qui agit sur les caractères.

[Traduit par la Rédaction]

Introduction

Slight, random departures from bilateral symmetry can result from environmental or genetic stress during development (Palmer and Strobeck 1986; Møller and Swaddle 1997;

Imasheva et al. 1999) and may represent the ability of a genotype to produce an optimal phenotype (Møller and Thornhill 1997; Gangestad and Thornhill 1999; Shykoff and Møller 1999). Such fluctuating asymmetry (FA) is often inversely related to fitness (Møller 1997; but see Clarke 1998a) and can also vary with the size and variability of morphological characters (Soule and Cuzin-Roudy 1982; Møller and Pomiankowski 1993; Møller 1994; Kodric-Brown 1997; Clarke 1998b; Woods et al. 1999; Reimchen and Nosil 2001).

Relationships between FA and trait size can be indicative of different modes of selection acting on morphological characters (Møller and Pomiankowski 1993). Continuously distributed morphological traits under stabilizing selection often exhibit low levels of FA and a characteristically

Received November 22, 2000. Accepted April 19, 2001.
Published on the NRC Research Press Web site at
<http://cjz.nrc.ca> on June 25, 2001.

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U-shaped or flat relationship between the size of the trait and its level of FA (Møller and Pomiankowski 1993; Møller 1994). Individuals near the mean size or value for such traits have low FA, whereas extreme phenotypes at the tails of the frequency distribution have higher levels of FA than modal phenotypes (Soule and Cuzin-Roudy 1982; Kodric-Brown 1997; Reimchen and Nosil 2001; but see Woods et al. 1999). Alternatively, traits under directional selection often exhibit a negative or positive slope when trait size is regressed against FA (Møller 1990, 1992; Møller and Pomiankowski 1993; but see Tomkins and Simmons 1995) and have high levels of FA (Møller and Høglund 1991; Dufour and Weatherhead 1996; Møller and Zamora-Munoz 1997; but see Balmford et al. 1993, Bjorksten et al. 2000).

The water boatmen *Callicorixa vulnerata* are sexually size-dimorphic (i.e., females are larger than males) aquatic insects often inhabiting small ponds (Hungerford 1948; Nosil 2001). Field collections and experimental results with this species revealed mid-leg tarsal FA (tarsal spine number and tarsal length) was inversely related to survival, feeding ability, and nutritional condition, possibly because of poorer genetic quality in highly asymmetrical individuals or the performance costs associated with tarsal asymmetry (Nosil and Reimchen 2001). This inverse association between FA and components of fitness was independent of trait size and occurred in both sexes.

The mid-legs of corixids are morphologically specialized to facilitate attachment to bottom substrate during underwater feeding. Such morphological characters in which asymmetry or other forms of variability directly compromise performance or fitness could be under strong stabilizing selection for size and (or) symmetry (i.e., constancy) (Møller 1991; Balmford et al. 1993; Møller and Pomiankowski 1993; Crespi and Vanderkist 1997; Clarke 1998b). Also, there is no a priori reason to suspect that mid-leg tarsal traits are sexually selected and subject to consistent directional selection during mating. Consequently, mid-leg tarsal traits in male and female *C. vulnerata* are predicted to exhibit patterns of FA with respect to trait size that are indicative of stabilizing selection, with extreme phenotypes exhibiting increased levels of FA relative to modal phenotypes (cf. Soule and Cuzin-Roudy 1982). However, given the size dimorphism in *C. vulnerata* it may be expected that different modes or intensities of selection act on the same characters in each sex (e.g., Fairbairn and Preziosi 1996). Associations between FA and trait size may also reflect such differences between the sexes (cf. Bortolotti and Gabrielson 1995).

Materials and methods

During July 1999, adult *C. vulnerata* (males, $n = 211$; females, $n = 156$) were captured from Rithet's bog in Victoria, B.C. (48°25'N 123°19'W), using dip nets. Morphometric methods are described in detail elsewhere (Nosil and Reimchen 2001). Each individual was sexed, measured for body length, and weighed (both wet and dry mass were recorded). On each left and right mid-leg, the tarsi were measured and tarsal spines counted. Signed asymmetry was calculated as the difference in length and spine number of the right and left tarsi ($R - L$). Unsigned absolute asymmetry was calculated as the absolute value of signed asymmetry, whereas unsigned relative asymmetry was calculated as the absolute value of $(R - L)/[(R + L)/2]$. Tarsal length and tarsal spine number were

calculated as the average of the right and left measurements. The coefficients of variation (CV) for asymmetry were calculated as SD/mean .

The statistical characteristics of tarsal asymmetry have also been described in detail elsewhere (Nosil and Reimchen 2001). In both traits, significant nondirectional asymmetry relative to measurement error was detected (side \times individual interactions, all $p < 0.001$; see Palmer 1994). Mean-signed spine number asymmetry and mean-signed tarsal length asymmetry did not differ significantly from zero, indicating no evidence of directional asymmetry. Both traits departed statistically from normality, but the distribution of asymmetry in both traits was leptokurtic, consistent with FA and not antisymmetry.

I tested whether extreme phenotypes exhibit higher levels of FA in each sex separately (ingroup-outgroup (IG-OG) effect; Soule and Cuzin-Roudy 1982). The distributions of trait size for both tarsal spine number and tarsal length were standardized (Z scores; Sokal and Rohlf 1981) and trait-size values within one standard deviation of the mean were assigned to an IG (i.e., modal phenotypes), whereas trait values greater than one standard deviation above or below the mean were assigned to a high outgroup (HOG) or low outgroup (LOG), respectively. The HOG and LOG were pooled to yield a combined OG (i.e., extreme phenotypes). Kruskal-Wallis ANOVA was used to test for variability in absolute FA between extreme and modal phenotypes (IG-OG effect).

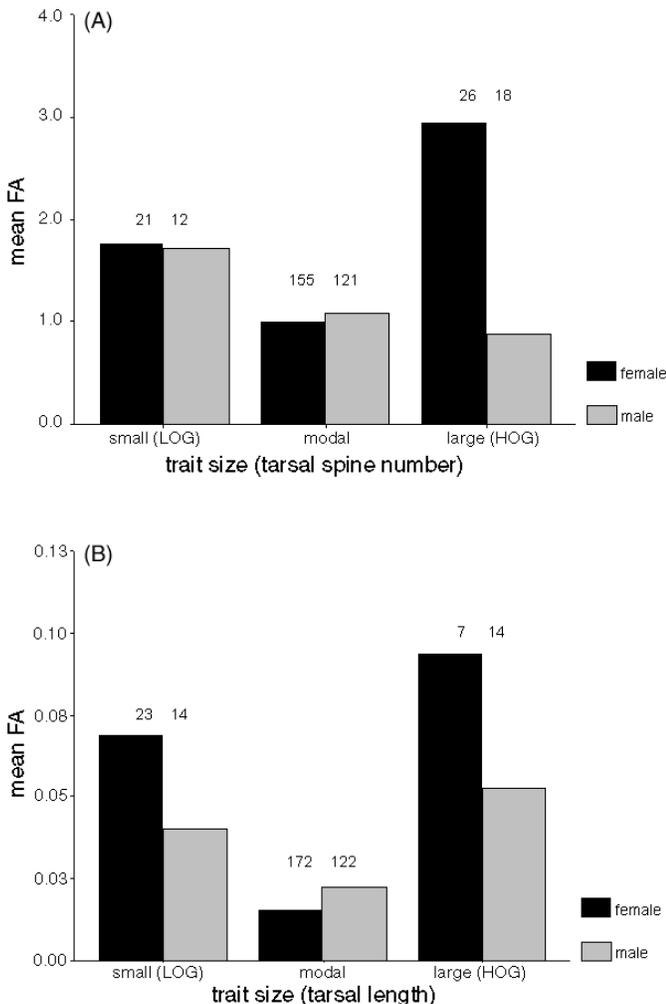
I tested for linear and U-shaped relationships between trait size and FA in each sex using regression coefficients (β) and coefficients of determination (r^2) from linear and second-order polynomial regressions, respectively (FA as the dependent variable). For the full quadratic model, both linear and quadratic regression coefficients are presented. A significant negative linear term and a significant positive quadratic term in the full quadratic model would indicate a U-shaped relationship between FA and trait size. I test for the significance of β using the t ratio ($\beta/SE \beta$) and test for the significance of r^2 using the F ratio ($MS_{\text{regression}}/MS_{\text{residual}}$), where MS is the mean squares of the regression and residual terms. Although the distribution of FA is characteristically half-normal, regression analysis is robust to violation of the assumption of normally distributed errors (Sokal and Rohlf 1981) and results using nonparametric Spearman's rank correlation were similar to those from linear regression.

To assess the overall importance of quadratic components in males and females, I fit models with only linear components and then fit models with both linear and quadratic (pairwise products of character deviations from the mean) components. I used partial F tests to assess the increase in statistical fit when quadratic components were added to the model (Norusis 1993). I tested whether linear and quadratic regression coefficients differed statistically between the sexes using a generalized linear model (FA as the dependent variable) with sex as a factor and trait size as a covariate. Estimates for quadratic regression coefficients include both linear and quadratic components of a trait, thus accounting for the effects of linear regression coefficients (cf. Lande and Arnold 1983). A significant sex \times trait interaction indicates that the regression coefficients differ between the sexes (test for homogeneity of slopes, ANCOVA). As each interaction tests the same hypothesis, significance levels from these interactions were corrected for multiple comparisons using the sequential Bonferroni method (Rice 1989). All statistics were run using SPSS (version 9.0; SPSS Inc., Chicago).

Results

After grouping into extreme and modal trait-size categories, extreme phenotypes for both mid-leg tarsal spine number and mid-leg tarsal length tended to exhibit higher levels

Fig. 1. Mean tarsal FA for *Calliicorixa vulnerata* with mid-leg tarsal trait sizes within (IG, modal phenotypes), above (HOG), and below (LOG) one standard deviation of the population mean; tarsal spine number FA (A) and tarsal length FA (B). Extremely small and large phenotypes (LOG and HOG, respectively) tended to exhibit higher levels of tarsal FA than modal phenotypes. However, differences were statistically significant only in females (see text for statistical tests). Mean values are shown for illustrative purposes. Sample sizes are shown above the bars.



of FA than modal phenotypes (Fig. 1). However, differences in FA levels between extreme and modal phenotypes were significant only in females (females: spine number FA, $\chi^2_1 = 8.51$, $p < 0.01$ and tarsal length FA, $\chi^2_1 = 6.55$, $p < 0.05$; males: spine number FA, $\chi^2_1 = 1.32$, $p = 0.17$ and tarsal length FA, $\chi^2_1 = 1.86$, $p = 0.17$; Kruskal–Wallis ANOVA). For tarsal spine number in males, individuals with extremely small trait sizes had markedly higher levels of FA than individuals with modal or large trait sizes.

I then tested whether males and females differed in overall levels of FA or differed in associations between FA and trait size. Although the sexes did not differ in absolute or relative FA for either tarsal trait (all $p > 0.25$, Mann–Whitney U tests; Table 1), the relationship between FA and trait size did differ between males and females (Table 2).

In females, both linear and quadratic regression coeffi-

cients for tarsal spine number FA against trait size (number of spines per tarsus) were significant. However, there were significant increases in r^2 when quadratic components were added to the model (absolute spine number FA, $F_{[1,148]} = 72.92$, $p < 0.001$; relative spine number FA, $F_{[1,148]} = 22.88$, $p < 0.001$; partial F tests). For both relative and absolute tarsal length FA, no linear relationships between FA and trait size (tarsal length) were detected, whereas quadratic regression coefficients were significant in all cases. There were substantial increases in r^2 when quadratic components were added to the model (absolute tarsal length FA, $F_{[1,147]} = 30.77$, $p < 0.001$; relative tarsal length FA, $F_{[1,147]} = 36.91$, $p < 0.001$; partial F tests). In all four of the full quadratic models, the linear terms were significant and negative, whereas the quadratic terms were significant and positive, indicative of a U-shaped relationship between FA and trait size.

In males, three of four linear regression coefficients were significant and all four were negative. None of the quadratic regression coefficients were significant and increases in r^2 were slight when quadratic components were added to the regression model (absolute tarsal spine, $F_{[1,199]} = 0.61$, $p = 0.44$; relative spine number FA, $F_{[1,199]} = 3.68$, $p = 0.06$; absolute tarsal length FA, $F_{[1,199]} = 1.12$, $p = 0.21$; relative tarsal length FA, $F_{[1,199]} = 3.49$, $p = 0.06$; partial F tests).

I tested whether linear and quadratic regression coefficients of FA against trait size differed statistically between the sexes (sex \times trait interaction, see Methods). The linear regression coefficients for tarsal spine number differed statistically between the sexes, whereas the coefficients for tarsal length did not (absolute spine number FA, $F_{[1,353]} = 35.75$, $p < 0.01$; relative spine number FA, $F_{[1,352]} = 20.74$, $p < 0.01$; absolute tarsal length FA, $F_{[1,352]} = 1.81$, $p > 0.10$; relative tarsal length FA, $F_{[1,352]} = 0.03$, $p > 0.10$; ANCOVA). All four quadratic regression coefficients differed between the sexes (absolute spine number FA, $F_{[2,353]} = 67.88$, $p < 0.01$; relative spine number FA, $F_{[2,352]} = 22.41$, $p < 0.01$; absolute tarsal length FA, $F_{[2,352]} = 21.86$, $p < 0.01$; relative tarsal length FA, $F_{[2,352]} = 25.83$, $p < 0.01$; ANCOVA).

Discussion

Mid-leg tarsal FA was inversely related to fitness in *C. vulnerata* in a previous study and this fitness reduction was independent of trait size, body size, and sex (Nosil and Reimchen 2001). I predicted that extreme phenotypes in this species would exhibit increased FA, as is expected for traits under stabilizing selection (cf. Soule and Cuzin-Roudy 1982; Møller and Pomiankowski 1993). Consistent with the prediction, water boatmen with extremely large or extremely small tarsal traits tended to have higher levels of FA than modal phenotypes (IG–OG effect). Notably, this suggests selection against asymmetry per se will indirectly impose stabilizing selection on trait size.

Elevated FA in extreme phenotypes has also been documented in fish and other insects (Soule and Cuzin-Roudy 1982; Kodric-Brown 1997; Reimchen and Nosil 2001; but see Clarke 1993; Woods et al. 1999) and several explanations can account for such associations. Firstly, homozygosity has been linked to inferior developmental stability (Leary et al. 1984; Mitton 1993 for review; but see Clarke 1993) and Soule (1982) suggested homozygotes may be partitioned into

Table 1. Mean, standard deviation (SD), and coefficient of variation (CV) for mid-leg tarsal FA in male ($n = 211$) and female ($n = 156$) *Callicorixa vulnerata* from a natural population.

	Males			Females			Z
	Mean	SD	CV	Mean	SD	CV	
Absolute							
Spine number FA	1.12	1.20	1.07	1.28	2.05	1.60	-0.23
Tarsal length FA (mm)	0.03	0.05	1.67	0.03	0.07	2.33	-0.70
Relative							
Spine number FA	0.11	0.13	1.18	0.11	0.14	1.27	-0.47
Tarsal length FA (mm)	0.03	0.05	1.67	0.03	0.08	2.67	-0.70

Note: Also shown is the test statistic (Z scores) from Mann–Whitney U tests comparing median FA levels between the sexes. None of the differences are statistically significant (all $p > 0.25$).

Table 2. Linear and quadratic regression analyses of absolute and relative tarsal spine number FA and tarsal length FA on trait size (mid-leg spine number, mid-leg tarsal length) in male and female *C. vulnerata*.

	Females				Males			
	r^2	df	β_1 (SE β_1)	β_2 (SE β_2)	r^2	df	β_1 (SE β_1)	β_2 (SE β_2)
Absolute spine number FA								
Linear	0.18***	149	0.38 (0.07)***	—	0.01	200	-0.07 (0.04)	—
Quadratic	0.45***	148	-1.90 (0.27)***	0.09 (0.01)***	0.02	199	0.07 (0.18)	-0.01 (0.01)
Relative spine number FA								
Linear	0.03*	149	0.01 (0.01)*	—	0.09***	199	-0.02 (0.01)***	—
Quadratic	0.16***	148	-0.10 (0.02)***	0.01 (0.00)***	0.11***	198	-0.08 (0.03)*	0.00 (0.00)
Absolute tarsal length FA								
Linear	0.00	148	0.01 (0.05)	—	0.02*	200	-0.07 (0.03)*	—
Quadratic	0.17***	147	-2.22 (0.41)***	1.17 (0.21)***	0.03	199	-0.30 (0.22)	0.12 (0.11)
Relative tarsal length FA								
Linear	0.02	148	-0.10 (0.06)	—	0.05**	200	-0.11 (0.04)**	—
Quadratic	0.22***	147	-2.81 (0.45)***	1.42 (0.23)***	0.07**	199	-0.56 (0.24)*	0.23 (0.12)

Note: The significance of r^2 is tested using the F ratio ($MS_{\text{regression}}/MS_{\text{residual}}$), whereas the significance of β is tested using the t ratio ($\beta/SE \beta$). β_1 refers to the linear regression coefficient, whereas β_2 refers to the quadratic regression coefficient. There were significant increases in r^2 when quadratic components were added to linear models in females but not in males (see Results). The degrees of freedom (df) is for the residual MS and asterisks mark the significant test results (*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$).

the tails of the size distribution for some morphological characters. If water boatmen in the tails of the size distribution for tarsal traits are highly homozygous, relative to modal phenotypes, this may account for high levels of FA in extreme phenotypes. Alternatively, genotypes with extreme phenotypes may contain poorly balanced or poorly integrated genes (Thoday 1958) and exhibit weaker developmental stability as a result of such genetic imbalance (Clarke et al. 1992; for a review see Clarke 1993). Furthermore, if asymmetrical structures result in reduced performance (e.g., Møller 1991; Balmford et al. 1993; Nosil and Reimchen 2001), this may cause even greater stress during subsequent development. Conceivably, elevated FA in extreme phenotypes results from a combination of these factors.

Callicorixa vulnerata are sexually size-dimorphic (Nosil 2001), suggesting that different modes or intensities of selection may act on morphological characters in each sex (e.g., Fairbairn and Preziosi 1996). Consequently, levels of FA and associations between FA and trait size might be expected to differ between the sexes. For example, if developing a large trait requires a greater resource commitment than developing a smaller one (Møller 1995), or if the larger sex is less likely to secure adequate resources for optimal growth, then the larger of the two sexes may suffer greater stress during development and exhibit higher FA (Bortolotti and

Gabrielson 1995). Alternatively, if large body size translates into competitive superiority (e.g., Kodric-Brown 1993; Blanckenhorn et al. 1998), the larger sex may exhibit lower FA. Despite being size dimorphic, trait CVs and levels of FA did not differ substantially between the sexes in *C. vulnerata*. This result is contrary to the predictions above but suggests trait variability, rather than size, may be a predictor of trait-specific developmental stability (e.g., Clarke 1998b; Woods et al. 1999). The results of this study are in agreement with the empirical results of Bortolotti and Gabrielson (1995) who found no difference in skeletal FA between the sexes in sexually size-dimorphic American kestrels (*Falco sparverius*).

Although FA levels did not differ between the sexes, patterns of FA with respect to trait size did differ. As evidenced by linear and quadratic regression coefficients, the relationship between FA and trait size was U-shaped in females but generally flat and linear in males. Potentially, the intensity of selection acting on tarsal traits under field conditions differs between the sexes. For example, if stabilizing selection against extreme phenotypes from natural populations is stronger in males than in females this would result in extreme males being rare. If so, a relatively flat distribution of FA with respect to trait size would result when males are collected from the wild (Kodric-Brown 1997).

Alternatively, the mode of selection acting on tarsal traits differs between the sexes. According to FA theory, the patterns of FA with respect to trait size observed in this study suggest directional and stabilizing selection on tarsal traits in male and female water boatmen, respectively (cf. Møller and Pomiankowski 1993). Male water boatmen must cling to females with their limbs during copulation (Hungerford 1948) and may use limbs in battles for feeding spots and mating opportunities, as has been documented in other hemipterans (Eberhard 1998). Intense male–male competition in corixids (e.g., Aiken and Malatestinic 1995) may impose directional sexual or natural selection for increased size or symmetry on male tarsal traits. Such traits presumably have weakened developmental control and may be subject to a trade-off between size and symmetry (Swaddle and Witter 1994; Møller 1995; Møller and Swaddle 1997), and this trade-off can result in only the highest quality individuals being capable of large and symmetrical development (Møller 1990, 1994; Møller and Høglund 1991).

However, traits under directional selection are expected to have higher levels of FA than traits under stabilizing selection (Møller and Høglund 1991; Møller and Pomiankowski 1993; Møller 1994; Møller and Zamora-Munoz 1997; but see Balmford et al. 1993; Tomkins and Simmons 1995; Allen and Simmons 1996; Bjorksten et al. 2000), but tarsal traits in males did not exhibit higher levels of FA than homologous structures in females. Also, experimental results suggest mid-leg tarsal traits might be under directional selection in females but not in males during food-limited conditions (this does not exclude sexual selection; P. Nosil, unpublished data). Conceivably, associations between FA and trait size do not always reflect the mode of selection acting on a trait, and associations between FA and fitness cannot be used to infer the mode of selection acting on morphological traits per se (Tomkins and Simmons 1995). Predicting the overall mode of selection acting on a trait is difficult, as selection can vary in both time and space (Endler 1986; Arnqvist 1992; Reimchen 1995; Preziosi and Fairbairn 1997).

In summary, the results of this study are generally consistent with the prediction that extreme phenotypes will exhibit higher levels of FA (cf. Soule and Cuzin-Roudy 1982). Further research could be directed at determining the causes of higher FA in extreme phenotypes and of the differences between the sexes. As departures from symmetry can impose functional costs resulting in reduced competitive ability (Møller 1997; Nosil and Reimchen 2001), it is likely this work will require insight into the biomechanical and ecological significance of the traits examined.

Acknowledgments

T.E. Reimchen provided invaluable insight at every stage of this study. Thanks also to C. Bergstrom for discussion, C. Shea for helping with collection of specimens, Dr. G. Scudder for performing the species identification, and to two anonymous reviewers for constructive and thoughtful comments. The Natural Sciences and Engineering Research Council of Canada provided financial support through a postgraduate scholarship to the author.

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