TARSAL ASYMMETRY, NUTRITIONAL CONDITION, AND SURVIVAL IN WATER BOATMEN (*CALLICORIXA VULNERATA*)

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Abstract.—Fluctuating asymmetry (FA) has been used as a measure of developmental stability and may indicate individual phenotypic or genotypic quality. Using water boatmen (*Callicorixa vulnerata*) from a natural population, we examined the relationship between tarsal FA (tarsal spine number, tarsal length) and indices of body condition in two habitats. We used body weight and residual body weight (controlling for body length) as indices of condition because experimental food deprivation in water boatmen led to a reduction in each. We detected a negative relationship between FA and both indices of condition in two ecologically distinct pond habitats. We predicted this association was due to a negative relationship between FA and competitive feeding ability. Consequently, we examined associations between survival time and tarsal FA in *C. vulnerata* under resource-limited laboratory conditions. Univariate analyses revealed a negative correlation between survival and tarsal FA in each trait. Inclusion of survival time, body length, gender, tarsal spine number, tarsal length, and measures of FA into multivariate analyses revealed a negative correlation between survival and FA. Individuals with the greatest survival had higher nutritional condition than individuals that succumbed early in the experiment. Asymmetric individuals may suffer a foraging handicap as a result of the use of tarsi in feeding or they may be of poor genetic quality. Our results suggest elevated FA may limit resource acquisition and are consistent with the use of FA as a measure of fitness.

Key words.—Body size, Corixidae, ecological severity, fitness, fluctuating asymmetry, nutritional condition, survival.

Random differences between the left and right side of a bilaterally symmetrical trait can result from environmental or genetic stress during development (Palmer and Strobeck 1986; Clarke and McKenzie 1992; Imasheva et al. 1999). Levels of such fluctuating asymmetry (FA) may represent the ability of the genotype to buffer developmental errors, and thus to develop an optimal phenotype under suboptimal conditions (Møller and Thornhill 1997; Gangestad and Thornhill 1999; Shykoff and Møller 1999; but see Leamy 1997). Consequently, FA has been used as a measure of developmental stability (Van Valen 1962; Leary et al. 1992; Palmer 1994), and elevated levels of asymmetry have been linked to reduced fitness and to poor phenotypic or genotypic quality (Moodie and Reimchen 1976; Møller 1991, 1996; Thornhill 1992; Allen and Simmons 1996; Møller and Zamora-Munoz 1997; Reimchen 1997; Hunt et al. 1998; reviewed in Møller 1997; but see Clarke 1998). Such fitness reduction may arise from bad genes, where asymmetry is an indicator of poor overall genetic quality (Møller and Hoglund 1991; Møller 1994; Hunt et al. 1998; Shykoff and Møller 1999), or from the performance costs of phenotypic asymmetry (Møller 1991, 1996; Balmford et al. 1993; Gummer and Brigham 1995).

Reduced fitness can result from numerous causes, including poor nutritional condition (Marden and Waage 1990; Hakkarainen and Korpimakin 1993) and small body size (Chapman 1971; Anholt et al. 1991; Reid and Roitberg 1995; Blanckenhorn et al. 1998). These factors reflect reduced individual quality, and thus FA should be negatively correlated with nutritional condition, body weight, and body size (e.g., Uetz and Smith 1999; Badyaev et al. 2000). However, such associations between FA and measures of quality or fitness

may be accentuated under severe ecological conditions (e.g., Moodie and Reimchen 1976; Kodric-Brown 1997; Shykoff and Møller 1999).

Water boatmen, such as *Callicorixa vulnerata,* are detrivorous or zoophagous semiaquatic insects often inhabiting small ponds (Hungerford 1977). In this paper, we examine whether asymmetry in *C. vulnerata* collected from the field is inversely related to three potential measures of individual quality: body size, body weight, and nutritional condition (weight controlling for length). We compare the relationships in two ecologically contrasting habitats and predict the association will be accentuated in potentially severe habitat.

A negative relationship between body condition or size and FA could arise from a negative relationship between FA and competitive feeding ability. Alternatively, elevated levels of FA may indicate increased nutritional stress during development, as has been reported in birds (Swaddle and Witter 1994; Møller 1995) and insects (Imasheva et al. 1999). Despite the consequences of FA to fitness, the influence of FA on competitive interactions for trophic resources is largely unexplored. In this study, we also perform a laboratory feeding experiment and predict inverse associations between FA and survival under resource limitation.

MATERIALS AND METHODS

Rithet's bog, located in Victoria, British Columbia (48°25′N, 123°19′W) contains a diversity of shallow ponds, some of which dry up in the summer while others remain covered in up to 150 cm of water. We collected adult water boatmen from three ponds (hereafter pond 1, pond 2, pond 3) chosen to represent highly distinctive ecological characteristics. Dissolved oxygen (DO) and temperature readings, measured with a standard DO/temperature meter, were taken at 1200 h and 0100 h to represent daily maximum and min-

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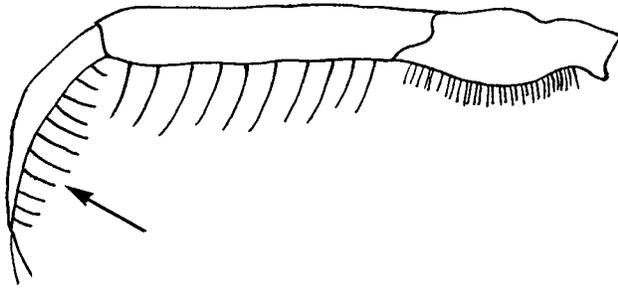
F$_{IG}$. 1. Typical midleg of a corixid (adapted from Thorp and Covich 1991). Tarsal spines shown by arrow. Magnification 40×.

imum. Water depth was measured in the center of the pond, and pond area was estimated using measuring tape. Distance to the road and to the nearest neighboring pond were also calculated for each site. Degree of shading was noted. Three-spine stickleback (*Gasterosteus aculeatus*) are a known predator of water boatmen (Jorgensen and Klemetson 1995; P. Nosil, per. obs.), thus, predatory stickleback densities were sampled by leaving minnow traps (four per site) baited with cheddar cheese in the water for 12-h periods on 15, 17, and 21 July. On each of these days, the traps were left from 0800 h to 2000 h, checked, reset immediately, and then checked once again the following morning at 0800 h (6 captures × 4 traps per site = 24 estimates per site). Stickleback were released back into the location where they were captured. Variability among ponds in *C. vulnerata* density and stickleback density was assessed using ANOVA.

To experimentally evaluate the relationship between food deprivation and weights loss, adult *C. vulnerata* ($n = 55$) were captured from pond 3 (5 July 1999), taken to the laboratory, and placed in a treatment group (food deprivation, $n = 31$) or a control group (food supplied, $n = 24$). Both groups were kept in plastic containers (50 cm × 30 cm × 25 cm) at ambient room temperature (18–24°C) for the duration of the experiment. The control group was kept in 2 L of unfiltered pond water and supplied with detritus (1.0 L), while the treatment group was kept in 2 L filtered pond water (0.45 μm filter). Every 24 h, dead individuals were collected and fixed in 10% formalin. The experiment was continued until all the individuals in the food-deprived group had died, at which stage live individuals in the control group were fixed. Specimens were measured for body length under a dissecting microscope (using an ocular micrometer at 10× magnification). Each individual was placed in a separate, labeled glass tube and dried in an oven at 60°C until constant weight was achieved. Each specimen was weighed (± 0.001 mg) and then sexed (40×) by eighth abdominal segment asymmetry (Hungerford 1977). Each specimen was also measured for midleg tarsal length, and tarsal spine number was counted on the left and right midleg (Fig. 1) using an ocular micrometer under a dissecting scope at 80×. We used an ANCOVA, with sex and treatment as factors, to test whether log weight at a given log length differed between the treatment and control group of water boatmen. The interaction between sex and treatment was also tested.

To assess potential associations between asymmetry, body size, and nutritional condition under field conditions, adult

C. vulnerata were captured (17 July 1999) from pond 1 ($n = 102$) and pond 2 ($n = 72$) with dipnets and were immediately preserved (10% formalin). To experimentally evaluate the relationship between asymmetry and survival under resource-limited conditions, we collected an additional 145 adult *C. vulnerata* from pond 1 and these were taken to the laboratory. The 102 individuals from pond 1 who were immediately fixed in 10% formalin acted as a control (time zero) for this experiment. The remainder of the individuals from pond 1 were taken to the laboratory and placed in a glass aquarium (60 cm × 30 cm × 30 cm), along with unfiltered pond water (depth 8 cm). Detritus (0.2 L) from the pond was added to the tank. At 1000 h and 1700 h each day, dead individuals were removed from the aquarium and fixed in 10% formalin. The experiment was run until all the individuals had died. The field preserved and experimental specimens were then measured for body length, dried, weighed, and had their tarsal traits (length, spine number) measured as outlined above. Replicate measurements were made on 50 individuals from pond 1 to assess measurement error. A few individuals had one or more tarsal traits damaged or could not be sexed and therefore were excluded from further analyses. To reduce bias, all measurements were done blind, without knowledge of collecting site, length, weight, or sex and were carried out by one individual (P. Nosil). Signed tarsal length asymmetry and signed tarsal spine number asymmetry were then calculated as the difference between the right and left measurements for tarsal length and tarsal spine number respectively (R − L). Unsigned asymmetry was calculated as the absolute value of signed asymmetry.

Using the mixed-model ANOVA approach of Palmer (1994), we detected significant nondirectional asymmetry relative to measurement error for both traits (tarsal spine number asymmetry $F_{49,100} = 8.58$, $P < 0.001$; tarsal length asymmetry $F_{49,100} = 36.61$, $P < 0.001$; side × individual interactions). The statistical characteristics of signed tarsal spine number asymmetry and signed tarsal length asymmetry were further assessed for water boatmen from each of the three ponds (cf. Palmer and Strobeck 1986; Palmer 1994). We tested for directional asymmetry (DA) using one-sample *t*-tests and binomial tests, for antisymmetry (AS) using measures of platykurtism (Sokal and Rohlf 1981), and for departures from normality with one-sample Kolmogorov-Smirnov tests (KS). We detected no evidence of DA. Mean signed asymmetry in each trait was not significantly different from zero in any case and left-side departures from symmetry were as likely as right-side departures (Table 1). The distribution of asymmetry departed from normality in several cases, but was leptokurtic in all cases, consistent with FA, and not AS (Gangestad and Thornhill 1999). Pooling the data for the three ponds and two sexes yielded similar results (Table 1). Measures of asymmetry referred to in the remainder of the paper are absolute (unsigned) FA.

Potential associations between absolute FA and trait size were examined using bivariate correlation. Among all individuals, tarsal spine number and spine number FA were significantly positively correlated ($r = 0.24$, $P < 0.001$), whereas tarsal length and tarsal length FA were not ($r = -0.06$, $P = 0.28$). Consequently, we scaled tarsal spine number FA for trait size (R − L)/[(R + L)/2] and used these size-cor-

TABLE 1. Characteristics of signed (R − L) tarsal spine number asymmetry (Spinsymm) and tarsal length asymmetry (Lengsymm). Mean (SE) signed asymmetry and measures of skew (g_1) and kurtosis (g_2) are shown along with results of tests for normality and directionality.

	Trait	N	Mean (R − L)	SE	g_1	g_2	Z^1	t^2	Binomial tests[3]
Pond 1									
Females	Lengsymm	93	0.002	0.004	−4.60	35.19	3.49***	0.48	0.33
	Spinsymm	93	0.006	0.040	0.65	1.38	2.29***	0.41	0.50
Males	Lengsymm	141	−0.002	0.004	−3.50	31.05	3.92***	−0.43	0.50
	Spinsymm	140	−0.013	0.016	−0.67	2.98	2.06***	−0.78	0.46
Pond 2									
Females	Lengsymm	28	0.009	0.010	2.49	12.70	1.68**	0.91	0.36
	Spinsymm	29	0.016	0.028	1.07	3.08	1.06	0.57	0.44
Males	Lengsymm	36	−0.019	0.011	−0.58	1.46	1.19	−1.75	0.63
	Spinsymm	36	0.003	0.025	1.04	2.39	1.05	0.12	0.54
Pond 3									
Females	Lengsymm	29	−0.002	0.026	−0.04	6.23	1.62*	−0.09	0.38
	Spinsymm	29	−0.091	0.054	−0.87	1.56	1.13	−1.70	0.67
Males	Lengsymm	25	−0.010	0.013	1.45	7.30	1.60*	−0.76	0.63
	Spinsymm	25	−0.007	0.023	−1.00	3.22	1.22	−0.30	0.54
Pooled	Lengsymm	369	−0.002	0.003	−0.65	20.14	5.81***	−0.48	0.48
	Spinsymm	369	−0.015	0.010	1.00	4.94	3.68***	−1.48	0.54

[1] Test statistic from Kolmogorov-Smirnov tests for normality.
[2] Test statistic from one-sample *t*-tests, all $P > 0.05$.
[3] Proportion of left-side departures from symmetry, all $P > 0.05$.
* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

rected tarsal spine number FA scores in all subsequent analyses. Notably, tarsal length FA and tarsal spine number FA were significantly correlated (Spearman's $\rho = 0.23$, $P < 0.001$). We also performed analyses using a composite FA index (CFA), which was found to be the least biased and the most powerful CFA when FA distributions were leptokurtic (CFA 3, Leung et al. 2000). To calculate this index, FA values of individuals were ranked for each trait and the ranked values for the two traits summed to give a CFA value for each individual. For tied ranks, individuals were assigned the mean rank.

For the specimens preserved immediately after capture, we used ANCOVA analyses to test for relationships between measures of body size or condition (dependent variable) and FA (covariate). Pond number and sex were included as factors in the model to determine whether any such relationships differed between the two ponds or between the sexes (test for homogeneity of slopes). Although sex was included as a factor in all analyses, none of the interaction terms with sex were either significant (all $P > 0.25$) or of primary interest in this study, and thus are not reported. We performed two separate analyses for each index of quality. The first analysis included measures of FA for each of the two tarsal traits, whereas the second analysis used the CFA.

For the results of the feeding experiment, we used Spearman rank correlation (SR) and multiple regression analyses to test for associations between FA and survival time. When morphology (body length, tarsal length, tarsal spine number) and FA (tarsal spine number FA, tarsal length FA) were regressed against survival, the slopes did not differ between the genders in any case (sex × tarsal spine number FA, $F_{1,132} = 0.08$, $P = 0.78$; sex × tarsal length FA, $F_{1,132} = 1.43$, $P = 0.23$; sex × body length, $F_{1,132} = 0.08$, $P = 0.78$; sex × tarsal spine number, $F_{1,132} = 0.04$, $P = 0.84$; sex × tarsal length, $F_{1,132} = 0.35$, $P = 0.55$; *F*-ratio interactions, AN-

COVA). Consequently, sex was coded as a binary variable (females = 0, males = 1) and included in the multivariate analysis of survival time (Norusis 1993). Examination of residual plots indicates none of the assumptions of regression analysis appeared to be violated. The distribution of the residuals did not depart from normality ($Z = 1.01$, $P = 0.26$; one-sample Kolmogorov-Smirnov test). For univariate comparisons using single traits, we corrected significance levels for the number of traits examined (Bonferroni method; Rice 1989). All statistics were run using SPSS (ver. 9.0).

To help visualize the form of selection acting on FA during the feeding experiment, we calculated univariate fitness functions using the nonparametric cubic spline approach of Schluter (1988). This technique does not assume any a priori form of selection on a character and may detect local optima not readily detectable with parametric regression techniques. Fitness functions and standard errors (based on bootstrap resampling) from 1000 bootstraps were calculated for the FA in each trait on a program provided by D. Schluter (GLMS, ver. 3).

RESULTS

Pond Characteristics

The three ponds differed in most habitat characteristics, and water boatmen from these ponds also exhibited morphological variability (Tables 2, 3). Pond 2 differed markedly from ponds 1 and 3 in having potentially more severe ecological conditions. Specifically, pond 2 exhibited greater temperature fluctuations, higher maximum temperature, smaller area, lower water depth, higher exposure to sunlight, and increased isolation relative to the other sample ponds. There was significant variability among ponds in conspecific density ($F_{2,72} = 27.95$, $P < 0.001$; ANOVA) and in predatory stickleback density ($F_{2,125} = 134.11$, $P < 0.001$; ANOVA),

TABLE 2. Habitat variables for the three sample ponds in Rithet's bog used in the study. There was significant variability among ponds in conspecific density and in predatory stickleback density ($P < 0.001$; ANOVA).

Variable	Pond 1	Pond 2	Pond 3
Temperature (°C)			
High	17	27	18
Low	16	14	16
Range	1	13	2
pH	6.95	6.97	7.01
Dissolved oxygen (ppm)	2.0	7.0	2.4
Water depth (cm)	55	7	68
Pond area (m²)	86	21	48
Mean conspecific density (per 3000 cm³)	1.04 (SD = 2.14)	9.20 (3.74)	0.85 (1.35)
Stickleback density (mean number per trap)	2.00 (SD = 3.08)	11.33 (3.14)	5.45 (6.16)
Exposure to sunlight	low (shaded)	high (open)	low (shaded)
Distance from roadway (m)	155	10	145
Distance to nearest pond (m)	5	145	27

with pond 2 exhibiting higher conspecific density and higher stickleback density than pond 1 ($P < 0.05$, post-hoc Bonferroni test).

Fluctuating Asymmetry, Body Size, and Nutritional Condition

We experimentally evaluated the relationship between food deprivation and weight loss. Water boatmen deprived of food in the laboratory survived an average of 2.2 days (range 1–5 days) and exhibited a 27.1% reduction in average dry weight relative to the control group (2.99 vs. 4.10 mg respectively, $t_{53} = 3.50$, $P < 0.001$; t-test on raw numbers). The control group did not suffer any mortality. Log weight increased with log body length in individuals sampled from the field ($r = 0.64$, $P < 0.001$; $n = 174$; Pearson's correlation); thus, we examined differences in weight between the treatment (food deprived) and control group (food provided) while statistically controlling for body length. The slopes of

the log weight versus log length regression did not differ between the treatment and the control or between the sexes (treatment × length, $F_{1,55} = 0.95$, $P = 0.33$; sex × length, $F_{1,55} = 0.42$, $P = 0.52$; ANCOVA test of parallelism). However, the treatment group exhibited lower log weight for a given log length relative to the control group (treatment, $F_{1,55} = 22.10$, $P < 0.001$; Fig. 2), with no differences between the sexes (sex, $F_{1,55} = 0.39$, $P = 0.53$; sex × treatment, $F_{1,55} = 0.21$, $P = 0.65$). Consequently, to reduce variance due to body length, we used the residuals from a log weight versus log length regression as an index of overall of nutritional condition in subsequent analyses.

We examined associations between FA, body weight, nutritional condition, and body length in water boatmen captured from ponds 1 and 2, which differed in ecological characteristics. We predicted inverse relationships between tarsal FA and measures of body size or condition and also predicted such associations would be accentuated under the potentially

TABLE 3. Mean (SD) trait sizes and fluctuating asymmetry (FA) levels for male and female *Callicorixa vulnerata* collected from three ponds in Rithet's bog.

| Trait	Pond 1	Pond 2	Pond 3
Body length (mm)			
Females	7.77 (0.61)	7.64 (0.82)	7.73 (0.77)
Males	7.38 (0.67)	7.12 (0.70)	7.43 (0.53)
Dry weight (mg)			
Females	4.17 (1.47)	4.45 (2.00)	n/a
Males	3.46 (1.20)	3.12 (0.92)	n/a
Tarsal spine number			
Females	10.76 (1.54)	12.55 (2.75)	11.28 (3.20)
Males	10.10 (1.89)	11.99 (2.58)	11.60 (1.37)
Tarsal length (mm)			
Females	0.96 (0.07)	0.91 (0.16)	0.93 (0.11)
Males	0.94 (0.10)	0.83 (0.10)	0.91 (0.06)
Tarsal length FA			
Females	0.016 (0.036)	0.022 (0.048)	0.071 (0.120)
Males	0.019 (0.042)	0.046 (0.050)	0.034 (0.058)
Spine number FA			
Females	0.090 (0.104)	0.100 (0.110)	0.186 (0.236)
Males	0.123 (0.146)	0.103 (0.108)	0.070 (0.089)
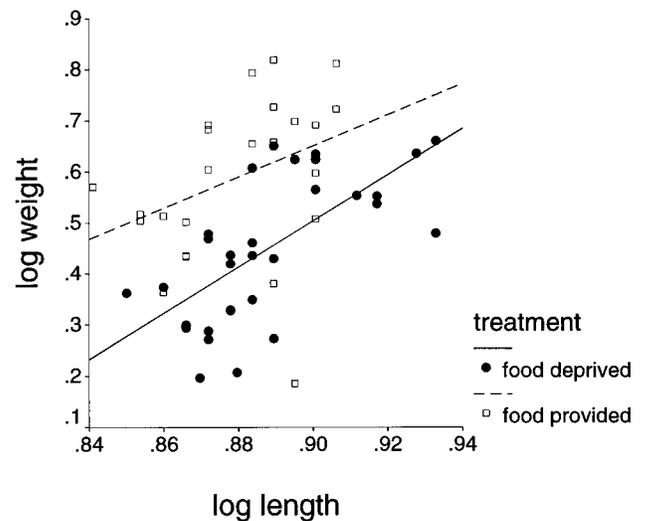
FIG. 2. Log weight versus log length for a treatment (experimentally food deprived) and a control (food provided) group of *Callicorixa vulnerata*. The slopes of the regression do not differ between the treatment and the control but differences in elevation (y-intercept) are statistically significant ($P < 0.001$; ANCOVA). Treatment: $y = 4.53x - 3.57$. Control: $y = 3.05x - 0.21$.

TABLE 4. Results of ANCOVA testing for linear associations between fluctuating asymmetry (FA; covariate) and indices of body size (log weight, log length) and an index of nutritional condition (residuals from a log weight vs. log length regression). Results are shown for an analysis including FA values from each of the two traits measured (tarsal length FA, tarsal spine number FA) and from an analysis using a composite FA index (CFA, see Materials and Methods). The CFA was negatively related to log weight and to nutritional condition. These associations did not differ between the two sample ponds used in the study or between the sexes (see Results for statistical tests).

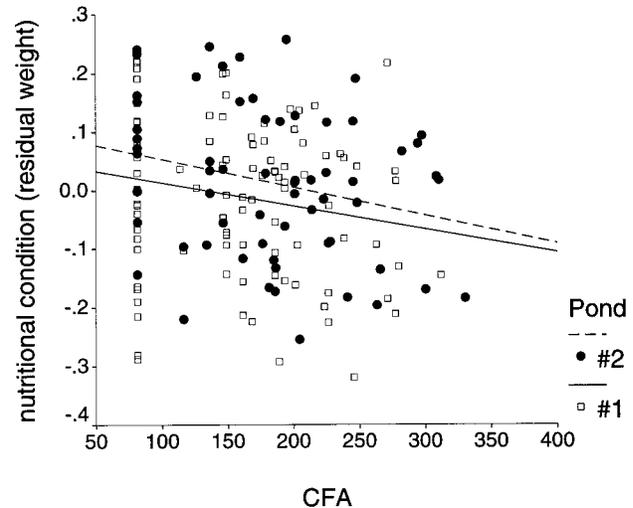|	B	SE B	$F_{1,165}$	P
Log weight (mg)				
Tarsal length FA	−0.50	0.30	2.80	0.09
Tarsal spine number FA	−0.23	0.10	4.77	0.03
CFA	−0.01	0.00	10.98	0.001
Log length (mm)				
Tarsal length FA	−0.22	0.07	8.74	0.004
Tarsal spine number FA	0.01	0.03	0.17	0.68
CFA	−0.01	0.00	3.49	0.06
Residual weight				
Tarsal length FA	−0.08	0.27	0.08	0.78
Tarsal spine number FA	−0.25	0.09	7.13	0.008
CFA	−0.01	0.00	7.12	0.008

FIG. 3. Relationship between nutritional condition (residuals from a log weight vs. log length regression) and an index of asymmetry (CFA) in *Callicorixa vulnerata* captured from two ecologically distinct ponds (pond 1, 2) in Rithet's bog (see Table 2 for pond characteristics). The inverse relationship is significant ($P < 0.01$; ANCOVA) overall and the slopes of the regression do not differ between ponds.

severe ecological conditions detected in pond 2. Results for log weight and for nutritional condition were generally consistent with the first prediction. Tarsal spine number FA, tarsal length FA, and CFA were negatively related to log weight (Table 4). However, these inverse relationships between FA and log weight did not differ between ponds in any case (tarsal length FA, $F_{1,165} = 0.95$, $P = 0.33$; tarsal spine number FA, $F_{1,165} = 0.01$, $P = 0.93$; CFA, $F_{1,165} = 0.56$, $P = 0.46$; test for homogeneity of slopes, ANCOVA). There was a significant negative relationship between FA and nutritional condition for tarsal spine number FA and for CFA (both $P < 0.01$; Fig. 3), and these relationships did not differ between ponds (tarsal length FA, $F_{1,165} = 0.01$, $P = 0.94$; tarsal spine number FA, $F_{1,165} = 0.83$, $P = 0.36$; CFA, $F_{1,165} = 0.04$, $P = 0.85$).

We also predicted FA may be negatively related to body length. We detected a significant inverse relationship between FA and log body length for tarsal length FA only, but this relationship was dependent on the sample site (pond × tarsal length interaction, $F_{1,165} = 4.99$, $P < 0.05$, all other interactions, $P > 0.05$). The slope of the regression of log body length versus tarsal length FA was significantly different from zero for pond 2 (slope = −0.35, $t = −3.13$, $P < 0.01$; linear regression), but not for pond 1 (slope = −0.03, $t = −0.28$, $P = 0.78$). Notably, the inverse relationship between body length and CFA approached statistical significance ($P = 0.06$, Table 4).

Fluctuating Asymmetry and Survival

Results of the competition experiment revealed nonrandom survival time among phenotypes. Survival time (days) was inversely related to tarsal spine number FA ($\rho = −0.21$, $P < 0.05$, $n = 133$; SR), tarsal length FA ($\rho = −0.25$, $P < 0.01$, $n = 133$; SR), and CFA ($\rho = −0.25$, $P < 0.01$, $n = 133$; SR). A fitness function derived using the cubic spline technique shows a steady decline in survival time with in-

creasing FA for both traits examined (Fig. 4). We suspected that morphological traits such as body length, trait size (tarsal spine number, tarsal length), and gender might influence competitive interactions and possibly confound associations between FA and survival. When partial associations among morphological variables were accounted for in a multivariate analysis, FA in each trait was negatively correlated with survival (tarsal spine number FA, partial $r = −0.19$, $t = −2.21$, $P < 0.05$; tarsal length FA, partial $r = −0.16$, $t = −1.83$, $P = 0.07$; multiple regression). Replacing the two single-trait measures of FA with the CFA yielded a similar result, with survival time being negatively correlated to CFA (partial $r = −0.26$, $t = −3.02$, $P < 0.01$; multiple regression).

Individuals dying in the later stages of the experiment exhibited higher condition (residual weight) than those succumbing earlier (Fig. 5). We compared the nutritional condition of the time 0 group to that of the experimental group for different survival times (time 0, days 1–3, days 4–5, days 6+). Sex was included as a factor in the model and tarsal spine number FA and tarsal length FA were included as covariates. The variability in condition among groups (time 0, days 1–3, days 4–5, days 6+) was highly significant compared to variation within groups ($F_{3,233} = 17.01$, $P < 0.001$; ANCOVA) and this effect was not dependent on sex or on FA (survival time × sex, $F_{3,233} = 0.66$, $P = 0.58$; survival time × tarsal spine number FA, $F_{3,233} = 0.91$, $P = 0.44$; survival time × tarsal length FA, $F_{3,233} = 0.20$, $P = 0.90$; ANCOVA interaction terms). Specifically, individuals dying during the first 5 days exhibited markedly lower condition than the time 0 group, whereas there was little difference in condition between the time 0 group and those with the greatest survival (days 6+).

DISCUSSION

Water boatmen collected from the field differed in weight, nutritional condition, and levels of FA. Consistent with our
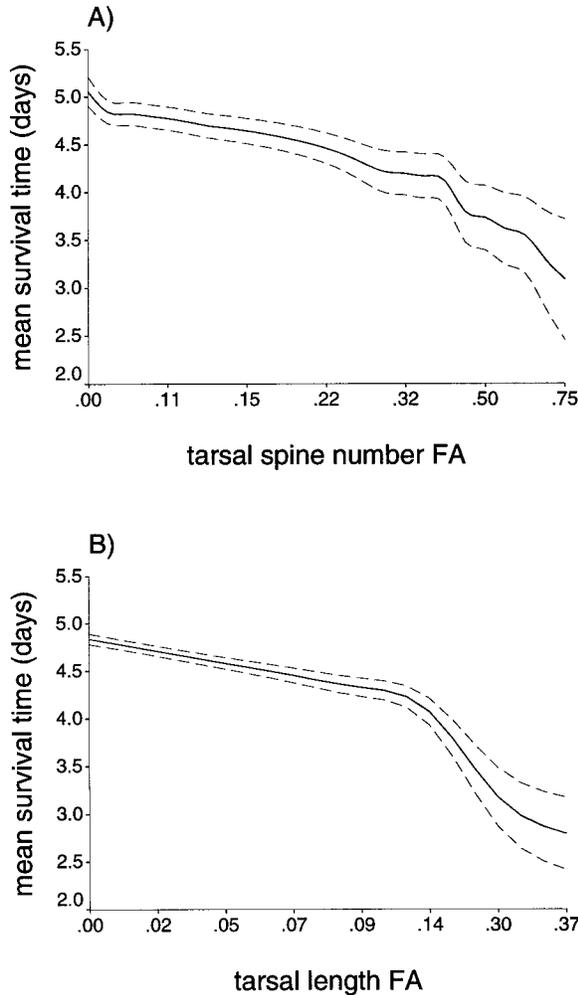
A)

B)

FIG. 4. Relationship between fluctuating asymmetry (FA) in two traits (tarsal spine number, tarsal length) and survival during a laboratory feeding experiment. Shown are fitness functions (solid line) and bootstrap SE (dashed lines, 1000 replicates) based on nonparametric regressions using the cubic spline technique (Schluter 1988). Increasing FA in each trait led to a steady and significant decrease in survival time (days). (A) tarsal spine number FA; (B) tarsal length FA.

prediction, there was an inverse relationship between weight and FA and nutritional condition and FA. Similar results have been reported in shrews (Badyaev et al. 2000). We predicted that such an association was due to differential feeding ability, with increased FA resulting in decreased competitive ability. Consistent with this suggestion, FA was negatively related to survival in the laboratory feeding experiment. Other studies have also detected a negative association between FA and survival in insects (Thornhill 1992; Naugler and Leech 1994; Ueno 1994), and our results are consistent with general hypotheses linking FA to reduced fitness (Møller 1997; but see Clarke 1998).

FA is a reflection of the exposure to environmental or genetic stress during development (Swaddle and Witter 1994; Imasheva et al. 1999), as well as the ability of the genotype to develop an optimal phenotype in the face of such stress (reviewed in Møller and Thornhill 1997; Shykoff and Møller
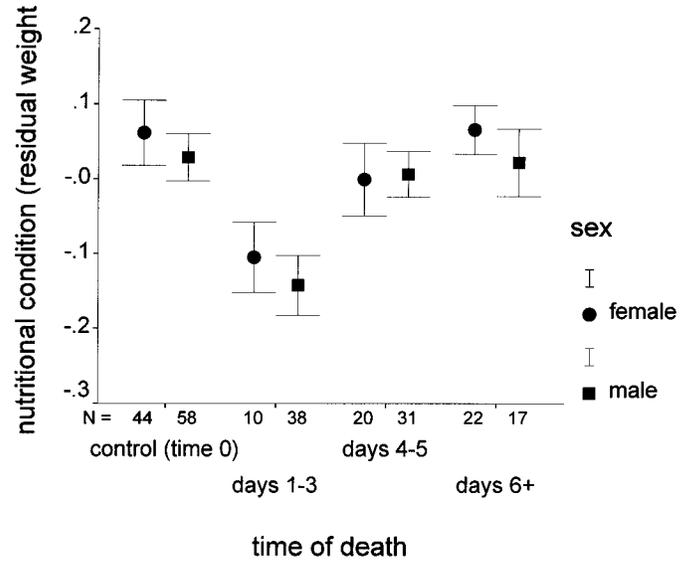

FIG. 5. Mean ($\pm$ 95% CI) nutritional condition (residuals from a log weight vs. log length regression) at death for *Callicorixa vulnerata* from a control group (time 0) and for individuals dying in three consecutive stages of the feeding experiment. Individuals succumbing earlier in the experiment had lower condition than those succumbing later.

1999). For example, an inverse relationship between nutritional condition and FA may arise from physiological stress resulting from food deprivation inducing FA or from highly asymmetric individuals having reduced competitive feeding ability. However, these explanations for relationships between FA and quality are not mutually exclusive, because poor environmental conditions may work in conjunction with poor developmental stability to produce asymmetrical phenotypes (Møller 1995).

Weak or nonexistent associations between FA and condition may arise if lower-quality individuals are capable of producing highly symmetrical phenotypes under benign conditions or if in less competitive environments lower-quality individuals are not subjected to greater stress during development than higher-quality individuals (Møller 1995). Thus, FA may be a poor predictor of overall quality when trait ontogeny takes place under benign conditions (Shykoff and Møller 1999). Alternatively, differences in quality or condition between individuals differing in levels of FA, who differ in competitive ability, may arise only in highly competitive environments. However, our results demonstrate FA was related to nutritional condition in two habitats differing in densities of predatory fish, range of temperature fluctuations, and pond size, which suggests that such FA associations can occur across a range of ecological conditions. Further research could be directed at investigating relationships between FA and fitness among ecologically distinct environments.

Nutritional stress resulting in elevated FA has been observed in a diverse range of taxa including insects, birds, and mammals (Sciulli et al. 1979; Swaddle and Witter 1994; Møller 1995; Imasheva et al. 1999). The processes leading to nutritional stress may be multiple and include competitive interactions, predation risk, and resource availability. In

blackbirds (*Turdus merula*), less-fit phenotypes may be displaced into marginal habitat, resulting in food deprivation and a consequent increase in FA (Møller 1995). Aquatic insects may reduce foraging rates or shift into suboptimal habitat in response to predation risk, leading to increased nutritional stress (for review, see Dill 1987). This may occur in corixids (Oscarson 1987), and, if so, provides one plausible mechanism for the relationship between FA and nutritional condition observed in the present study.

Alternatively, highly asymmetric water boatmen may have inferior competitive ability and exhibit lower nutritional condition as a result of poor foraging ability. FA has been linked to decreased competitive ability in other insects (Thornhill 1992; Allen and Simmons 1996; Møller and Zamora-Munoz 1997; Blanckenhorn et al. 1998). Tarsal FA was negatively correlated to survival of water boatmen in our feeding experiment, adding support to the hypothesis that the inverse relationship detected between FA and nutritional condition is due to differential feeding ability. Statistical removal of partial associations between morphology and FA did not obscure these associations between tarsal FA and survival.

The experimental conditions used in our feeding experiment may be representative of conditions in natural populations. For example, *C. vulnerata* are found in ponds as small as the experimental tank, and natural densities of *C. vulnerata* in the study population can be as high as those used in the experiment (P. Nosil, unpubl. data). Because our experiment did not have multiple treatment levels, it was not truly manipulative and it is not possible to determine the exact cause of mortality (Krebs 1989). However, because survival rate of the water boatmen was associated with nutritional condition, we suggest FA is inversely correlated with competitive feeding ability. For example, differences in competitive feeding ability among subpopulations of fish can lead to differences in nutritional condition (Siikavuopio et al. 1996).

Oxygen consumption and metabolic costs for insects may vary with the intensity of competition, food availability, and foraging activity (Peckarsky and Cowan 1992; Duvall and Williams 1995; Raubenheimer and Gade 1996; Jeeva et al. 1999). Water boatmen supplied unlimited food in the lab for 5 days suffered zero mortality and were in similar condition (residual weight) to the time 0 group used as a control in the feeding experiment (mean = 0.07, 0.04, respectively, t_{126} = -0.96, $P = 0.34$). This suggests water boatmen feed effectively enough under nonlimiting laboratory conditions to maintain residual weights similar to those observed in the field and to prevent mortality for at least 5 days. Water boatmen dying within first 5 days of the competitive feeding experiment exhibit significantly lower condition than individuals fed in the laboratory (mean = -0.07, 0.07, respectively, t_{124} = -4.72, $P < 0.001$) and time 0 individuals collected from the field. This reduction suggests these individuals could not compete effectively for limiting food resources and were unable to maintain metabolic activity. That these individuals exhibited the highest levels of FA is consistent with general predictions coupling asymmetry with reduced fitness (Reimchen 1997; reviewed in Møller 1997). However, we are not able to account for the mortality of water boatmen in later stages of the experiment because these did not show a marked reduction in condition. That these

individuals maintained residual weights similar to field-caught individuals and individuals provided unlimited food suggests these individuals were able to feed effectively despite resource limitations. Previous studies have shown similar trends involving FA and competition for mates such as in Japanese scorpion flies (Thornhill 1992), cerambycid beetles (Møller and Zamora-Munoz 1997), and dung flies (Allen and Simmons 1996).

Asymmetry is expected to influence performance directly (Balmford et al. 1993; Palmer 1994; Dufour and Weatherhead 1996; but see Leung and Forbes 1996) and, for example, may mechanically compromise function during copulation (Blanckenhorn et al. 1998) or flight (Møller 1991, 1996; Gummer and Brigham 1995; Crespi and Vanderkist 1997; McLachlan 1997). The relationship between tarsal asymmetry and reduced survival in water boatmen may reflect such performance costs and functional constraints (poor feeding or adhesion ability). Corixids use their midleg, including the tarsus, for locomotion and substrate adhesion (Chapman 1971). Tarsal spines may facilitate attachment to the substrate (Thorp and Kovich 1991; Merritt and Cummins 1996). Potentially, minor departures from symmetrical tarsi reduce locomotory or adhesive ability and result in performance reduction and this is most expressed during resource limitation.

It has also been suggested that increased FA reflects poor genetic quality (Møller 1990; Møller and Hoglund 1991; Hunt et al. 1998; Shykoff and Møller 1999), although this suggestion is controversial (Palmer 1994; Leamy 1997). The significant positive correlation between tarsal spine number FA and tarsal length FA observed in this study suggests FA-fitness relationships in water boatmen may result from general associations between genetic quality and FA. This is consistent with studies that found significant correlations among traits within individuals (Whitlock 1993; Møller 1994; Lens and van Dongen 1999), but is inconsistent with other studies that found no such within-individual correlations (Ryan et al. 1995; Brakefield and Breuker 1996). If FA is not a reliable indicator of underlying individual developmental stability, this might explain why several studies have not detected associations between FA and measures of fitness (e.g., Thornhill 1992; Ueno 1994; Leung and Forbes 1997; for review, see Clarke 1998). Indeed, even when within-individuals correlations in FA levels are detected they are often weak (e.g., Dufour and Weatherhead 1996) or examine only a suite of localized characters (e.g., Leamy 1993). Potentially, the correlation observed in this study may be due to similar ontogenetic timing between tarsal traits in their trait-specific susceptibility to stress, rather than FA signaling organism-wide developmental competence (Clarke 1995). Examining a greater number of characters, preferably from different regions of the body, could confirm whether within-individual FA levels among characters in water boatmen are concordant.

If tarsal asymmetry influences feeding ability in natural populations, water boatmen with elevated FA may suffer reduced fitness. The quantity and quality of food ingested by female insects relates directly to the efficiency of yolk synthesis, the number of eggs laid, and the viability of eggs (House 1963; Johanssen 1964; Chapman 1971); thus, reduced feeding ability can be expected to reduce fitness. In males, increased foraging ability should translate into increased

body size or greater nutrient reserves, both of which may increase fitness during sexual selection (Trivers 1976; Marden and Waage 1990; Anholt et al. 1991).

Numerous studies of FA have focused on indices of quality, sexual selection, and competition for mates (for review, see Møller and Swaddle 1997). We predicted an inverse relationship between nutritional condition and FA in water boatmen from natural populations and predicted such an association may be due to differential trophic competitive ability. We have identified an inverse relationship between nutritional condition and FA in field-caught *C. vulnerata* and an inverse relationship between FA and survival in a resource-depleted habitat. This suggests elevated FA may limit resource acquisition and is consistent with our hypothesis. Identifying the mechanism for such an association will require insight into the functional and the biomechanical significance of the measured traits.

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