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Fluctuating asymmetry and parasitism in six New Zealand insects

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Abstract – Positive associations between parasitic infections and developmental instability are often reported in the literature. In some cases, developmentally unstable individuals are of lower genetic quality and more prone to infection, whereas in other cases, parasites appear to directly cause developmental instability. We determined whether parasitism correlated with fluctuating asymmetry in femur length, a measure of developmental instability, in two species of cockroaches harbouring benign nematodes, and four species of grasshoppers infected with harmful gregarine protozoans. We found no evidence that the more asymmetrical individuals were more heavily parasitized, in either of the six insect species. These results provide several exceptions to the pattern generally reported in the recent literature, and suggest that, at least among insects, fluctuating asymmetry and parasitism are not always associated. © Elsevier, Paris

Cockroaches / fluctuating asymmetry / grasshoppers / gregarines / oxyuroid nematodes / parasitism

1. INTRODUCTION

The ability of a genotype to undergo stable development under given conditions, or developmental stability, is frequently assessed by the level of fluctuating asymmetry [11, 12, 14]. Fluctuating asymmetry, or FA, corresponds to the small and random differences between the right and left expressions of an otherwise bilaterally symmetrical character [18]. Several environmental and genetic stresses can lead to high levels of FA [8, 11]. These range from food shortages and pesticides to homozygosity and hybridization.

Parasitism is one of the most common environmental correlates of developmental instability, with high levels of FA being associated with parasitic infection [9]. The causes of the relationship are either that developmentally unstable individuals are in generally poor condition or have genetically determined poor resistance to parasites, or that parasitism itself imposes a physiological stress causing parasitized individuals to develop imperfectly. In other words, parasites can either be a consequence or a cause of FA. Whatever the underlying explanation, the relationship is ubiquitous. Møller [9] reviewed the literature and found that most studies on parasitism and developmental instability report a positive association between FA and parasitism. Interestingly, cases in which there was no relationship between FA and parasitism all involved insect hosts.

The present study determined whether FA was correlated with parasitic infections in six host-parasite systems involving New Zealand insects. More specifically, we related FA in hind femur length to parasitism by oxyuroid nematodes in two species of cockroaches, and by gregarine protozoans in four species of grasshoppers. We examined FA in femur length for two reasons. First, FA in leg length has been shown to be sensitive to parasitism in ground-dwelling insects [17], as has FA in wing size in flying insects [1, 3, 10]. These traits, though essential to locomotion and presumably under strong stabilizing selection, are in fact not only slightly unstable but also easy to measure. Second, we wanted a homologous trait present in all species to facilitate comparisons among them and the interpretation of these comparisons; bristles or spines were not appropriate for this purpose. Both types of parasite investigated here live in the gut of their hosts; they have direct life cycles, with infective stages exiting in the host's faeces to be ingested by new hosts. Hosts can thus become infected by both parasites from a very early age. Gregarines compete for nutrients with the host and/or damage the gut epithelium, often resulting in deleterious effects for the host [6, 21]. They are the sort of parasites that could cause developmental instability in infected hosts [9]. Oxyuroid nematodes, on the other hand, are considered benign to their hosts, at least the members of the family Thelastomatidae infecting New Zealand cockroaches [19, 20]. Here, we only tested for an association

between parasitism and FA. However, if parasitic infections are a consequence of FA, we would expect parasitized insects of all species to show higher FA than their uninfected conspecifics. On the other hand, if parasitic infections are a cause of FA, we would expect parasitized grasshoppers to be relatively more asymmetrical than parasitized cockroaches, because the gregarine parasites of grasshoppers are more harmful than the nematode parasites of roaches.

2. METHODS

Adult insects were collected from the Otago and Canterbury regions of the South Island, New Zealand, between mid-November 1996 and late January 1997. Coleopteran and dipteran insect species were also sampled, but none were parasitized. The cockroaches included the blattellid *Parellipsidion pachycercum* Johns and the blattid *Celatoblatta quinque maculata* Johns. The grasshoppers consisted of three species of Acrididae, *Sigaui obelisci* Bigelow, *Paprides dugdali* Bigelow and *Phaulacridium marginale* Walker, and the tettigoniid *Concephalus bilineatus* Erichson. Because of the patchy distribution of the different insect species, they were collected from different localities ranging from native forest to high-altitude tussock grassland. Cockroaches were collected by hand from the undersides of adjacent rocks or logs, whereas grasshoppers were captured over a small area using hand nets. All conspecific insects were collected on the same day, therefore spatial and temporal influences are unlikely to affect our results.

Insects were sacrificed in jars containing chloroform. Right and left hind femora of the third leg pair were detached from the insects' bodies and kept separately, allowing dissections and leg measurements to be performed independently by two different investigators. All nematodes found in the gut of cockroaches and all gregarines found in grasshoppers were counted. No effort was made to identify the parasite species involved. These tend to be host-specific (e.g. [19, 20]) and all parasites from the same host sample were of a single morphological type and appeared to belong to the same species.

Measurements of all femora were taken from identical points on the leg. Femora lengths were variable between conspecific individuals and particularly between species. Assuming that for a given precision, asymmetry is easier to detect in large femora than in small ones, we corrected for this effect by adjusting with the zoom of a dissecting microscope the length of all left femora to 80 units on the micrometer in the eyepiece. Asymmetry was then calculated as the small positive or negative departure of the right femur length from 80 units. Femur length ranged from 3 to 8 mm among the insect species studied; the precision

afforded by our 1/80th unit was thus comparable to that used in other studies of FA in insect body parts in which significant results were obtained (e.g. [1, 3]). These differences represent relative FA in femur length, corrected for average femur length and with the precision standardized across insect species of different sizes. This procedure was adopted since we wanted results of a precision comparable across species. Each femur was measured twice on separate occasions. The repeatability of femur measurements and their asymmetry was extremely high and statistically significant ($r^2 = 0.99$, $P < 0.0001$ in all cases), suggesting that the precision of the measurements was very high and appropriate for FA analyses.

We tested for the presence of either directional asymmetry and/or anti-symmetry in our data [10, 13]. Femur length did not show directional asymmetry since mean signed left-minus-right values for each sample did not deviate significantly from zero (one-sample t -tests, $P > 0.05$ in all cases). Also, femur length did not demonstrate anti-symmetry since the frequency distributions of signed left-minus-right values in each sample did not depart from a normal distribution (one-sample Kolmogorov-Smirnov tests, $P > 0.05$ in all cases). We tested for sex differences in FA using the randomization procedure described below and found none; therefore, we pooled male and female insects of the same species for further analyses.

Three analyses were performed on the FA data. First, we compared the mean FA of parasitized and unparasitized insects of the same species using a randomization procedure [7, 16]. This approach is ideal for FA data as it makes no assumption about the distribution of the data or the equality of variances between groups. The observed difference between the mean FA values of the two groups is one of many possible outcomes that could have arisen by chance. Using the RT 2.0 program (B. Manly, Centre for Applications of Statistics and Mathematics, University of Otago, New Zealand), we generated 20 000 possible outcomes by rearranging the FA data randomly between the unparasitized and parasitized groups and by calculating the difference between their means for each iteration. The significance of the observed difference is equal to the proportion of iterations that gave a more extreme difference than the observed one [16]. We calculated the power of these comparisons between two groups using standard formulae [5]. Second, we compared the proportions of symmetrical individuals, i.e. those individuals for which FA = 0, among parasitized and unparasitized insects of the same species, using Fisher's exact tests. This should allow any slight qualitative trend to be detected, even if the quantitative difference itself is very small. Third, we tested for a relationship between FA and parasite load using Spearman's rank correlations, separately for

Table I. Relative fluctuating asymmetry in hind femur length in parasitized and unparasitized individuals of 6 insect species; the percentage of asymmetrical individuals is shown in parentheses for each group.

Insect species	Unparasitized		Parasitized		Mean load (range)
	mean FA \pm SD (%)	<i>n</i>	mean FA \pm SD (%)	<i>n</i>	
Cockroaches					
<i>Parellipsidion pachycercum</i>	0.42 \pm 0.75 (36.8)	19	0.52 \pm 1.12 (24.4)	33	1.6 (1–3)
<i>Celatoblatta quinquemaculata</i>	0.24 \pm 0.45 (26.1)	23	0.49 \pm 1.08 (31.1)	45	1.4 (1–3)
Grasshoppers					
<i>Sigaus obelisci</i>	0.43 \pm 0.75 (45.5)	79	0.40 \pm 0.41 (55.3)	38	26.8 (1–220)
<i>Paprides dugdali</i>	0.22 \pm 0.36 (37.5)	16	0.25 \pm 0.37 (35.7)	28	12.7 (1–87)
<i>Phaulacridium marginale</i>	0.28 \pm 0.47 (26.1)	46	0.22 \pm 0.41 (26.7)	30	6.6 (1–18)
<i>Concephalus bilineatus</i>	0.22 \pm 0.50 (21.7)	23	0.39 \pm 0.50 (42.9)	28	5.7 (1–20)

each of the six insect species. Together, these three types of analyses should be able to detect the relationship between FA and parasitism, weak or strong, if it exists.

3. RESULTS

Following dissections and measurements, some individual insects were excluded from further analyses. Apart from those with missing or damaged hind femora, we also excluded one individual each from the *S. obelisci* and *P. dugdali* samples because they showed extreme asymmetry in femur length; these were probably the result of incomplete regeneration following leg loss. Four *P. pachycercum* and seven *C. quinquemaculata* were also excluded because they harboured gregarines (all other parasitized cockroaches harboured nematodes), as were three *C. bilineatus* that contained large hairworms (Nematomorpha).

Among the remaining insects, there was no evidence of a relationship between parasitism and FA in femur length (table I). There were no differences in mean FA between parasitized and unparasitized conspecifics (randomization tests, $P > 0.05$ in all cases). It is important to note that the power of these tests was relatively good for two species, *C. quinquemaculata* and *C. bilineatus* (power = 0.75 and 0.80, respectively), but low for the other four (between 0.50 and 0.60). The proportion of symmetrical individuals did not differ between parasitized and unparasitized insects (Fischer's exact tests, $P > 0.10$ in all species; table I). Finally, there were no correlations between parasite load and FA in femur length (Spearman's rank correlations, $P > 0.15$ in all species).

4. DISCUSSION

For a variety of reasons, we may expect higher levels of parasitism in developmentally unstable host individuals. In the only available synthesis of the literature, Møller [9] found that positive associations between parasitism and fluctuating asymmetry had indeed been reported in most published studies. Insect studies provided the only exceptions. Here, we failed to find any significant association between parasitism and FA in six different insect-parasite systems. Our measurements were precise and highly repeatable, and we used robust statistical analyses on decent sample sizes (44–117 individuals per host species). Although some tests had low statistical power, i.e. a low probability of rejecting a false null hypothesis, there is no reason to believe that our results are confounded by measurement error.

If the link between parasitism and FA is almost universal, as suggested by the results reviewed by Møller [9], and even if our low-power tests yielded correct results, then our findings could be exceptions in need of an explanation. A possibility may be that parasite loads were on average too low to cause measurable FA in our host samples. Oxyuroid nematodes in cockroaches regulate their population size and only occur in low numbers in infected hosts [19, 20]. Gregarines can be extremely numerous in some insects, but actually occurred in low numbers in two of our four grasshopper samples. It is also possible that the parasites investigated here are not harmful enough to be associated with increased FA. This could be true of nematodes but probably not of gregarines (see [6, 21]). The above arguments only apply to the case where parasites cause asymmetry; if high levels of FA reflect a higher susceptibility to parasite infections, then we would expect a positive association between para-

sitism and FA to emerge in all our study systems. Two other phenomena could mask any relation between FA and parasitism. First, highly-asymmetrical individuals could experience high mortality rates; if they are also heavily-parasitized then their loss from the population would weaken the relationship between FA and parasitism and make it difficult to detect. Second, if the parasite loads of the adults we collected do not reflect the loads these individuals harboured earlier in their development, we may expect no relationship between FA and parasitism among adults. Other studies (reviewed in Møller [9]) using a sampling approach similar to ours have found differences in FA between parasitized and non-parasitized hosts, and therefore the two above phenomena may often be not important enough to mask the difference.

Another possibility is that the relationship between parasitism and FA is not as general as suggested by previously published results. There has been a recent debate over the importance of publication biases in our understanding of ecological processes [2, 4, 15]. Most investigations of FA focus on a single host species; if their results do not match the predictions prevailing in the literature of the moment, they are likely to be blamed on measurement error and remain unpublished in a file drawer. The results we present here come from six independent host-parasite systems, and the absence of significant relationships cannot simply be attributed to methodological flaws. These results as a whole provide several exceptions to the universality of the association between parasitism and FA, at least among insects. Furthermore, they suggest that any interpretation based solely on the proportion of studies reporting a positive association may be misleading.

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