Adaptive wing asymmetry in males of the speckled wood butterfly (*Pararge aegeria*)?

Jack J. Windig and Sören Nylin[*]

Department of Zoology, University of Stockholm, 106 91 Stockholm, Sweden

We analysed asymmetry in the wings of the speckled wood butterfly (*Pararge aegeria*) by measuring area, length and width of fore- and hindwings. The type of asymmetry is fluctuating except for fore- and hindwing area, and forewing width in males, where asymmetry is directional. The amount of asymmetry (variance of the left wing minus the right wing) is less in males than in females. Within males asymmetry was directional and less in pale, predominantly territorial males than in melanic, predominantly non-territorial males. Asymmetry was negatively related to growth rate within females, but not within males. Females grew faster than males, but had higher asymmetry, whereas the more asymmetrical melanic males grew more slowly than pale males. The differences in the type and amount of asymmetry between the sexes and colour classes suggest a relationship with sex-specific flight patterns such as the territorial spiralling flight of males. We hypothesize that slightly asymmetrical males turn faster, and therefore are superior in territorial disputes over more symmetrical or extremely asymmetrical males. This implies that sexual selection via male–male competition influences the type and amount of asymmetry. The existence of more extremely asymmetrical individuals in females, and to a lesser extent in non-territorial males, may indicate that there are costs in reducing asymmetry.

Keywords: butterfly wings; directional asymmetry; flight performance; fluctuating asymmetry; sex differences; territorial behaviour

1. INTRODUCTION

Three types of asymmetry can be distinguished: fluctuating, directional and anti-symmetry (Van Valen 1962). Fluctuating asymmetry (FA) is defined as small random departures from anticipated bilateral symmetry (Markow 1995). In directional asymmetry (DA) the departures are not random, but biased to one side so that on average either the left or the right side is larger. In antisymmetry there is also a tendency for one of the sides to be larger, but half of the individuals are larger on the left and the other on the right, so that on average both sides are equal. The distinction between the three types is important: both directional asymmetry and antisymmetry are thought to be adaptive and caused by genetic differences, whereas fluctuating asymmetry is thought to reflect developmental stability (Palmer 1994; but see Graham *et al.* 1993).

Whether FA is to a large extent heritable and reflects quality at the individual level is controversial (pro: Møller & Swaddle 1997; Møller & Thornhill 1997*a*,*b*, 1998; Møller 1997; contra: Clarke 1998; Markow 1997; Palmer 1999; Palmer & Strobeck 1997; Whitlock & Fowler 1997). Both proponents and opponents agree that in order to be reliable studies of asymmetry must be performed carefully, especially because the amount of asymmetry is usually very small. Palmer & Strobeck (1986) and Palmer (1994) give three criteria that studies of asymmetry should fulfil, as follows.

(i) An assessment must be made of measurement error. FA is, by definition, small, and it can therefore have a size similar to that of measurement error. Because measurement error fluctuates between left and right, it is easily confounded with FA.

(ii) The amount of asymmetry may be related to trait size (see, for example, Windig 1998). If so, then this effect must be controlled; otherwise, a relationship between FA and quality may be entirely due to trait size.

(iii) The type of asymmetry must be determined. In directional and anti-symmetry a number of the indices used to quantify FA are not reliable. Moreover, non-fluctuating asymmetry may be under natural selection.

In fluctuating asymmetry, natural selection may also play a role. The best documented cases are the wings and tails of birds. Møller (1992) reported that males of the swallow (*Hirundo rustica*) with symmetrical wings and symmetrical, elongated tail feathers were preferred by females. Balmford *et al.* (1993), however, reported that more symmetrical males are aerodynamically superior, and that female preference might well be for better flyers instead of against asymmetrical males. In insects, information on the relationship between asymmetry and flight performance is scarce (but see McLachlan 1997). Here we report on asymmetry in the wings of the speckled wood butterfly. We test whether asymmetry differs between males and females, and between males that differ in territorial behaviour.
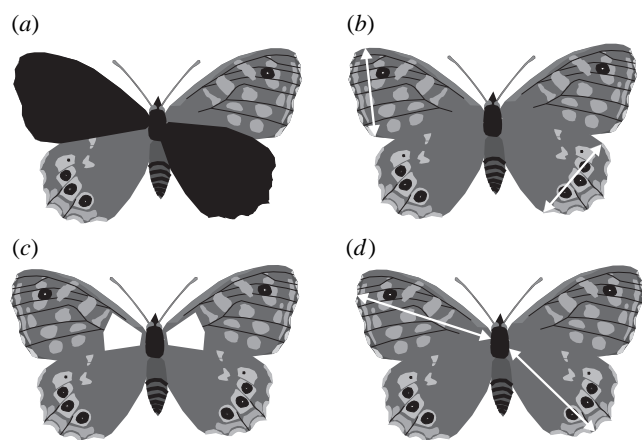
Figure 1. Measurements made for the analysis of wing asymmetry: (*a*) area; (*b*) width; (*c*) colour; (*d*) length. All measurements were made on both left and right wings, but colour was averaged over both sides.

2. METHODS

(a) *Study species and breeding*

The study species was the Southern European subspecies of the speckled wood butterfly, *Parage aegeria aegeria*. The individuals used in this study were the first two generations raised in the laboratory from 22 females caught in November 1997 around Funchal on the Atlantic island of Madeira (Portugal). First-generation larvae were raised individually on tufts, and second-generation larvae in pairs on potted plants (second generation) of the grass *Dactylis glomerata*. Altogether 359 adults with fully intact wings, needed for reliable analysis of asymmetry, were raised.

(b) *Measurement of traits*

The area, length and width of each of the fore- and hindwings were analysed (figure 1). Wing length was measured from the root of the wing to where the vein R5 (forewing) or Cu2 (hindwing) reached the edge. Wing width was measured along the edge of the wing from vein 2V to R3 (forewing) or 2V to Rs (hindwing) (see Mason *et al.* (1967) for the position of the veins). An image analyser consisting of a JVC TK 5066E camera and a Leica image analysis system was used for the measurements. Measurements were performed semi-automatically with the help of a program written in the Qwin image analysis software (produced by Leica, Cambridge, UK). Wings were detached from the body before measurement, by carefully cutting their connection to the body at the root of the wings. The program automatically thresholded a wing from the background for the area measurement (area is calculated by the number of pixels converted to square millimetres). Start and end points for width and length were indicated manually on the monitor. Both were more than 400 pixels in length so that pixellation error (as warned of in Palmer (1994)) was not large. Measurement results were sent to a spreadsheet without the person operating the program being able to inspect them.

To quantify measurement error, 50 individuals were measured twice. The repeated measurement included frame grabbing. The largest source of error, especially for area and colour measurements, appeared to be variation in illumination. Because left and right wings were recorded sequentially with, at most, a minimal change in illumination, measurement error in

asymmetry was probably somewhat overestimated by the repeated measurements procedure. To minimize the influence of variation of illumination, light intensity was standardized at the start of each session by measuring the same wing until it reached a standard value. Care was taken to ensure that the directional asymmetry found in some traits was not the consequence of a slight bias in the system. Change in the order in which left and right wings were measured did not influence the asymmetry, nor did the position of the wings in the image, or whether wings were measured with the dorsal or the ventral side facing upwards.

The colour of the wings was measured in the basal part of the forewings. This part is the most important for thermoregulation (Kingsolver 1987; Wasserthal 1975). In *P. aegeria* two types of mate-locating behaviour occur: patrolling and perching (Van Dyck *et al.* 1997). These types of mate-locating behaviour are related to the basal colour of the wings. Pale males are predominantly territorial perchers: they defend sunny spots against other males. Dark males are predominantly patrollers: they patrol in the wood in search of females. The difference in colour is related to differences in thermoregulation needed in sunny spots and shaded woods (Van Dyck & Matthysen 1998). The colour of the wings was measured as the average grey value, which ranged from 0 (black) to 255 (white).

(c) *Statistical analysis*

Measurement error was analysed by the methods of Palmer & Strobeck (1986) and Palmer (1994). A repeated-measures ANOVA was employed for the 50 individuals that were measured twice, with individual, side, and their interaction as factors. The side mean square (MS) was divided by the interaction MS to obtain an *F*-value indicating whether significant directional asymmetry was present. Interaction MS divided by the error MS yielded *F*- and *p*-values, indicating whether the asymmetry was significantly larger than measurement error. Kurtosis was calculated to test for the presence of platykurtosis, which is an indication of antisymmetry. From the mean squares in the ANOVA the FA10 index of Palmer (1994) was calculated; this index gives half the variance of the signed difference between left and right (L−R) corrected for measurement error. The uncorrected variance (FA4 of Palmer 1994) was also calculated, both for the 50 individuals measured twice, and for all 359 individuals. FA3, the average unsigned difference between left and right, or asymmetry as a percentage of trait size, was also calculated to facilitate comparisons with other studies. All calculations were performed separately for males and females.

The relationship between colour and asymmetry was analysed in two ways. To take into account the continuous nature of both colour and asymmetry the correlation between the absolute value of L−R and colour was calculated for the entire sample of males. A similar analysis is described by Rowe *et al.* (1997), to analyse the relationship between asymmetry and trait size, although they report that such an analysis has a low power of detecting a relationship. There is no gap that clearly demarcates territorial and non-territorial males. To be on the safe side we assumed that the most melanic quartile were non-territorial males whereas the palest quartile were territorial males. Amount of asymmetry measured as the variance of L−R was compared by an *F*-test for pale and melanic males. The average L−R was compared with a *t*-test to test for a difference in directional asymmetry.

Table 1. *Reliability of asymmetry measurements*

(ANOVA refers to the results of a repeated-measurement ANOVA on 50 individuals that were measured twice. Abbreviations: m, male; f, female. Significance of the individual indicates that the differences between individuals are larger than the measurement error; significance of side indicates the presence of directional asymmetry; significance of the individual × side interaction indicates that the FA is larger than the measurement error. Effect trait size refers to the correlation coefficient between trait size ($0.5 \times$ left + right) and asymmetry (absolute value of left − right).)

| | | ANOVA | | | | | | effect trait size | |
| | | individual | | side | | ind. × side | | | |
		F	p	F	p	F	p	r	p
area									
fore	m	4906.80	****	8.34	0.0081**	38.11	****	0.009	0.29
	f	413.19	****	0.01	0.99	8.05	****	−0.148	0.07
hind	m	10689.0	****	8.41	0.0081**	72.87	****	0.019	0.83
	f	3034.88	****	2.49	0.13	25.16	****	−0.038	0.64
length									
fore	m	320.61	****	0.11	0.74	11.83	****	−0.067	0.42
	f	374.47	****	0.46	0.51	15.09	****	−0.029	0.71
hind	m	162.05	****	0.43	0.52	3.67	0.0001	−0.069	0.40
	f	194.54	****	0.23	0.64	5.64	****	−0.092	0.25
width									
fore	m	174.11	****	6.85	0.015*	7.20	****	0.067	0.41
	f	84.26	****	0.59	0.46	7.84	****	−0.122	−0.14
hind	m	123.91	****	0.06	0.81	5.42	****	−0.146	0.07
	f	126.41	****	0.02	0.88	6.88	****	−0.156	0.05

$^*p < 0.05$; $^{**}p < 0.01$; $^{****}p < 0.0001$.

Table 2. *Comparison of asymmetry in males and females*

(Abbreviations: m, male; f, female. Mean trait size, average of the left and right wings; DA (directional asymmetry), average of signed difference between the left and right wings; FA3, average of unsigned difference between the left and right wings as a percentage of trait size (values in parentheses indicate whether the index is calculated over the whole sample (359) or over the 50 individuals that were measured twice); FA4, variance of signed difference between the left and right wings. FA10, variance of signed difference corrected for measurement error; here $2 \times$ FA10 is given to make it comparable to FA4. Difference m − f refers to an F-test on FA4 (359). p-values were corrected for directional asymmetry.)

| | | | | asymmetry indices | | | | difference m − f | |
		mean trait size	DA	FA3 (359)	FA4 (50)	$2 \times$ FA10 (50)	FA4 (359)	F-value	p
area									
fore	m	156.19	−0.65	0.86%[a]	3.862	3.761	4.135	2.177	****
	f	170.71	−0.38	1.36%	9.475	8.626	9.040		
hind	m	172.30	−0.54	1.02%[a]	5.548	4.472	6.052	2.083	****
	f	182.22	−0.59	1.48%	9.306	8.934	12.606		
length									
fore	m	19.71	0.05	1.15%	0.0868	0.0795	0.0404	1.343	0.034*
	f	20.44	0.04	1.07%	0.1093	0.1026	0.0542		
hind	m	16.51	0.06	1.31%	0.0476	0.0343	0.0402	1.433	0.013*
	f	17.20	0.04	1.19%	0.0693	0.0593	0.0576		
width									
fore	m	12.31	−0.10	1.87%[a]	0.0452	0.0390	0.0657	1.207	0.122
	f	12.50	−0.03	1.75%	0.0689	0.0591	0.0793		
hind	m	13.86	0.06	1.23%	0.0591	0.0482	0.0619	0.801	0.084
	f	14.19	−0.05	1.58%	0.0469	0.0395	0.0496		

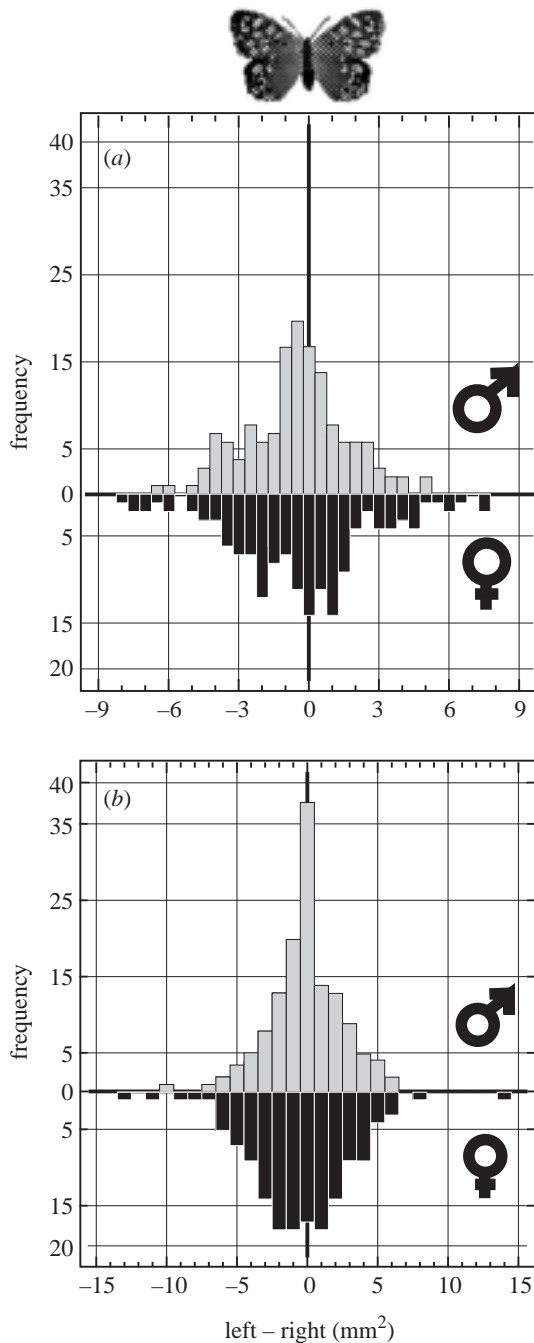$^*p < 0.05$; $^{****}p < 0.0001$.

Figure 2. Frequency distribution of the signed difference between the left and right area of forewings (*a*) and hindwings (*b*) for males (*n* = 187) and females (*n* = 172).

3. RESULTS

(a) *Type of asymmetry and measurement error*

For all traits measurement error was low compared with asymmetry (table 1). Directional asymmetry was significant only in males for forewing area, hindwing area, and forewing width. Correlation of asymmetry with trait size was not significant for any trait (table 1). Hence no correction for trait size was needed. Kurtosis was positive for all traits, so there was no evidence of antisymmetry.

(b) *Amount of asymmetry*

For all traits, asymmetry was about 1% of trait size and the difference between males and females was about
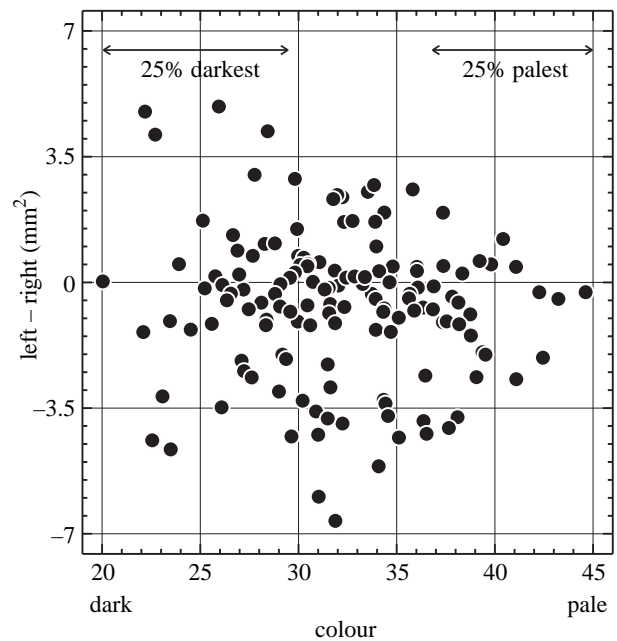

Figure 3. Relationship between asymmetry (signed difference between left and right wings) and colour, measured on a grey scale from zero (black) to 255 (white) for males. Quartiles of the palest and darkest males are indicated at the top of the figure.

ten times larger (table 2). Variance of L−R (FA4) was similar whether measured on the 50 repeated-measure individuals, or on all 359 individuals. Variances corrected for measurement error (FA10) were, on average, 4.2% lower for wing areas and 14.9% lower for linear measurements (table 2). The degree of asymmetry was significantly larger in females for wing areas and wing length (up to 7.5% of trait size), because extremely asymmetrical males do not exist, and because more males than females with an asymmetry close or equal to zero exist (figure 2).

(c) *Relationship with colour*

In males the asymmetry of wing area was related to colour. Despite its relatively low power, the correlation between colour and asymmetry was significant for forewing area (*r* = −0.1734, *p* = 0.0412; figure 3). It was not significant for hindwing area (*r* = −0.1056, *p* = 0.231). Asymmetry was on average larger in melanic males. The difference in asymmetry between the 25% darkest and 25% palest males (figure 3) was significant for forewing area (two-sided *F*-test: *F* = 2.125, *p* = 0.0280; figure 3), but not for hindwing area (*F* = 1.640, *p* = 0.1703). Directional asymmetry was not significantly higher in pale males (mean L−R: forewing area dark males −0.198, pale males −0.887, *t* = 1.419, *p* = 0.1605; hindwing area dark males −0.007, pale males −0.170, *t* = 0.308, *p* = 0.759). For all linear measurements and for all traits in females no relationship between colour and asymmetry could be detected.

4. DISCUSSION

Males and females of *P. aegeria* differ with respect to wing asymmetry in two ways: directional asymmetry occurs in males, but not in females, and the average

asymmetry is larger in females. The difference between the sexes is remarkable: there is no clear reason to expect differences between the sexes. In another butterfly, the peacock (*Inachis io*), no difference in FA was found between the sexes. Differences in FA between sexes in other organisms have been found. For example, Møller & Hoglund (1991) found that asymmetry was higher in males than in females in ornamental traits of birds, and Brückner (1976) and Clarke *et al*. (1992) found higher levels of asymmetry in male haploid bees than in diploid females. In butterflies haploidy–diploidy cannot explain the difference between sexes, because both sexes are diploid (females are the heterogametic sex). Speckled wood butterflies do not possess clearly ornamental traits, either, so the difference has to be explained elsewhere.

Differences in quality or fitness are often thought to be related to differences in FA (Møller & Swaddle 1997), although this relationship is not uncontroversial (see, for example, Clarke 1998). The fact that stress may increase asymmetry is less controversial (Whitlock & Fowler 1997). Fitness cannot differ between males and females, nor could the amount of food-plant stress differ between the sexes in this study, because they were raised simultaneously on the same food plants. However, growth rate may differ between the sexes, and growth rate in turn may influence FA (discussed in Clarke 1998; Møller 1997). In this study growth rate in the larval stage was significantly higher in females $(5.4\,\mathrm{mg\,d^{-1}})$ than in males $(4.9\,\mathrm{mg\,d^{-1}};\ t=4.98,\ p<0.0001)$. For the trait that differed most in FA between the sexes, forewing area, growth rate was significantly, negatively correlated with FA (unsigned difference between the left and the right wings) in females $(r=-0.187,\ p=0.0157)$, but not in males $(r=-0.008,\ p=0.920)$. The relationship of growth rate with FA is thus opposite across sexes and within females. The difference in the correlation of growth rate with FA between the sexes is intriguing; it suggests that males have mechanisms which avoid the production of extremely asymmetrical individuals even if their growth rate is slow.

The presence of directional asymmetry in males but not in females also indicates that a difference in asymmetry between the sexes is not merely a by-product of stress or of differences in growth rate. Palmer (1994) points out that adaptation is likely to be involved in directional asymmetry, and that these types of asymmetry are likely to be under genetic control. Interestingly, in bees there is also a difference between males and females in the shape of the wings; this difference is directional rather than fluctuating (Smith *et al*. 1997). Klingenberg *et al*. (1998) reported directional asymmetry for wings of several flies, but they did not distinguish between males and females. The presence of directional asymmetry in this study for forewing width, but not for forewing length, suggests that directional asymmetry is present in males not only for size, but also for shape.

The difference in asymmetry between pale, territorial males and melanic, non-territorial males resembles the difference between males and females. Non-territorial males are more asymmetrical, and asymmetry in territorial males tends to be directional, although the difference in directionality was not significant. Melanism in both the map butterfly (*Araschnia levana*) and the peacock

butterfly (*I. io*) is related to growth rate, possibly because of trade-offs (Windig 1999). The correlation between colour and growth rate is also significant in this study (males: $r=0.187$, $p=0.0172$; females: $r=0.344$, $p<0.0001$). The difference between pale and melanic males is, however, opposite to that between females and males: pale males have a high growth rate and low FA, whereas females have a high growth rate and high FA. The resemblance between asymmetry of melanic males and females may thus be linked to the absence of territorial behaviour in both females and melanic males.

Territorial males are frequently involved in disputes, in which they form so-called 'spinning wheels'. Two fighting males circle round each other and each tries to get on top to bounce the other male away (Austad *et al*. 1979; Wickman & Wiklund 1983). Fast flight and good manoeuvrability are thus very important for territorial males. A probable effect of variation in symmetry in wings in butterflies is that asymmetrical individuals cannot fly very well in a straight line. This implies, however, that they may make sharper turns in one direction. This, in turn, may give slightly asymmetrical males an advantage over symmetrical males in territorial disputes. This leads to the prediction that the direction of turning in males will be biased. A pilot analysis of films made in 1982 of *P. aegeria* from Sweden (Wickman & Wiklund 1983) showed no bias in the turns males made (89 clockwise, 72 anticlockwise $(\chi_1^2=1.795,\ p=0.180)$. This analysis included all the different flights that were made. However, the most relevant flight pattern, the 'spinning wheel' employed in territorial disputes, could only be analysed once. This one 'spinning wheel' consisted of ten clockwise turns and two in an anticlockwise direction. Turns in a spinning wheel are not independent: once the butterflies start turning in one direction, it is probably difficult to change the direction of turning. In future studies it therefore would be best to analyse the number of spinning wheels that turn predominantly in one or the other direction.

Relationships between wing asymmetry and flight performance have been evaluated for birds (Balmford *et al*. 1993; Swaddle 1997; Thomas 1993). Asymmetry leads to higher energetic costs of flight and poorer manoeuvrability. Butterflies fly, however, quite differently from birds. They have shorter and broader wings, and thus a low aspect ratio, compared with birds; this characteristic is associated with slower but more agile flight (Betts & Wootton 1988; Dudley & Srygley 1994). Moreover, they cannot adjust the area of their wings to compensate for asymmetry as birds can by spreading their wings and feathers more or less. Research on the relationship between asymmetry and flight in insects is scarce. Only McLachlan (1997) reports that in midges flight duration reduces, wing-beat frequency decreases and wing-beat amplitude increases when asymmetry is increased by snipping part of one of their wings. Mating success is also reduced in asymmetrical male midges.

This study underscores the importance of analysing whether asymmetry is directional rather than fluctuating before accepting asymmetry as a measure of quality. Indeed, it seems important to go one step further and first consider whether asymmetry (whether fluctuating or directional) itself might be under the influence of natural

selection. A likely, but maybe not the only, explanation for the DA found here is that it is an adaptation to flight in territorial disputes. It will be interesting to evaluate whether the difference in wing shape between males and females in bees (Smith *et al.* 1997) might be the consequence of natural selection rather than haploidy in males. The hypothesis that natural selection, because of flight performance in territorial disputes, has reduced asymmetry implies that there is a genetic basis for asymmetry. An interesting question then is why females and darkly coloured males have higher levels of asymmetry than territorial males. Systems must be operating that reduce asymmetry in pale males, but are not employed in females or dark males; this observation suggests that these systems are costly to operate, and thus that there may be a cost to symmetry. Finally, the practice of abandoning further research on a trait when directional asymmetry is found may prevent the uncovering of interesting relationships between natural selection and asymmetry.

REFERENCES

Austad, S., Jones, W. & Waser, P. 1979 Territorial defence in speckled wood butterflies: why does the resident always win? *Anim. Behav.* **27**, 960–961.

Balmford, A., Jones, I. J. & Thomas, A. L. R. 1993 On avian asymmetry: evidence of natural selection for symmetrical tails and wings in birds. *Proc. R. Soc. Lond.* B **252**, 245–251.

Betts, C. & Wootton, R. 1988 Wing shape and flight behaviour in butterflies (Lepidoptera: Papilionoidae and Hesperioidae): a preliminary analysis. *J. Exp. Biol.* **138**, 271–288.

Brückner, D. 1976 The influence of genetic variability on wing symmetry in honeybees (*Apis mellifera*). *Evolution* **30**, 100–108.

Clarke, G. M. 1998 Developmental stability and fitness: the evidence is not quite so clear. *Am. Nat.* **152**, 762–766.

Clarke, G. M., Oldroyd, B. P. & Hunt, P. 1992 The genetic basis of developmental stability in *Apis mellifera*: heterozygosity versus genic balance. *Evolution* **46**, 753–762.

Dudley, R. & Srygley, R. B. 1994 Flight physiology of neotropical butterflies: allometry of airspeeds during natural free flight. *J. Exp. Biol.* **191**, 125–139.

Graham, J. H., Freeman, D. C. & Emlen, J. M. 1993 Antisymmetry, directional symmetry, and dynamic morphogenesis. *Genetica* **89**, 121–137.

Kingsolver, J. G. 1987 Evolution of coadaptation of thermoregulatory behavior and wing pigmentation pattern in Pierid butterflies. *Evolution* **41**, 472–490.

Klingenberg, C. P., McIntyre, G. S. & Zaklan, S. D. 1998 Left–right asymmetry of fly wings and the evolution of body axes. *Proc. R. Soc. Lond.* B **265**, 1255–1259.

McLachlan, A. 1997 Size or symmetry: an experiment to determine which of the two accounts for mating success in male midges. *Ecoscience* **4**, 454–459.

Markow, T. A. 1995 Evolutionary ecology and developmental stability. *A. Rev. Entomol.* **40**, 105–120.

Markow, T. A. 1997 Meta-analysis of the heritability of developmental stability: a giant step backward. *J. Evol. Biol.* **10**, 31–37.

Mason, L. G., Ehrlich, P. R. & Emmel, T. C. 1967 The population biology of the butterfly, *Euphydryas editha*. V. Character clusters and asymmetry. *Evolution* **21**, 85–91.

Møller, A. P. 1992 Female swallow preference for symmetrical male sexual ornaments. *Nature* **357**, 238–240.

Møller, A. P. 1997 Developmental stability and fitness: a review. *Am. Nat.* **149**, 916–932.

Møller, A. P. & Hoglund, J. 1991 Patterns of fluctuating asymmetry in avian feather ornaments: implications for models of sexual selection. *Proc. R. Soc. Lond.* B **245**, 1–5.

Møller, A. P. & Swaddle, J. 1997 *Developmental stability and evolution.* Oxford University Press.

Møller, A. P. & Thornhill, R. 1997a Developmental stability is heritable. *J. Evol. Biol.* **10**, 69–76.

Møller, A. P. & Thornhill, R. 1997b A meta-analysis of the heritability of developmental stability. *J. Evol. Biol.* **10**, 1–16.

Møller, A. P. & Thornhill, R. 1998 Bilateral symmetry and sexual selection: a meta-analysis. *Am. Nat.* **151**, 174–192.

Palmer, A. 1999 Detecting publication bias in meta-analyses: a case study of fluctuating asymmetry and sexual selection. *Am. Nat.* (In the press.)

Palmer, A. R. 1994 Fluctuating asymmetry analyses: a primer. In *Developmental instability: its origins and evolutionary implications* (ed. T. A. Markow), pp. 335–364. Dordrecht, The Netherlands: Kluwer Academic Publishers.

Palmer, A. R. & Strobeck, C. 1986 Fluctuating asymmetry: measurements, analysis and pattern. *A. Rev. Ecol. Syst.* **17**, 391–421.

Palmer, A. R. & Strobeck, C. 1997 Fluctuating asymmetry and developmental stability: heritability of observable variation vs. heritability of inferred cause. *J. Evol. Biol.* **10**, 39–49.

Rowe, L., Repasky, R. R. & Palmer, A. R. 1997 Size-dependent asymmetry: fluctuating asymmetry versus antisymmetry and its relevance to condition-dependent signaling. *Evolution* **51**, 1401–1408.

Smith, D. R., Crespi, B. J. & Bookstein, F. L. 1997 Fluctuating asymmetry in the honey bee, *Apis mellifera*: effects of ploidy and hybridization. *J. Evol. Biol.* **10**, 551–574.

Swaddle, J. P. 1997 Within-individual changes in developmental stability affect flight performance. *Behav. Ecol.* **8**, 601–604.

Thomas, A. L. R. 1993 The aerodynamic costs of asymmetry in the wings and tail of birds—asymmetric birds can't fly round tight corners. *Proc. R. Soc. Lond.* B **254**, 181–189.

Van Dyck, H. & Matthysen, E. 1998 Thermoregulatory differences between the speckled wood butterfly: hot perchers and cold patrollers? *Oecologia* **114**, 326–334.

Van Dyck, H., Matthysen, E. & Dhondt, A. A. 1997 The effect of wing colour on male behavioural strategies in the speckled wood butterfly. *Anim. Behav.* **53**, 39–51.

Van Valen, L. 1962 A study of fluctuating asymmetry. *Evolution* **16**, 125–142.

Wasserthal, L. 1975 The role of butterfly wings in regulation of body temperature. *J. Insect Physiol.* **21**, 1921–1930.

Whitlock, M. C. & Fowler, K. 1997 The instability of studies of instability. *J. Evol. Biol.* **10**, 63–67.

Wickman, P.-O. & Wiklund, C. 1983 Territorial defence and its seasonal decline in the speckled wood butterfly (*Pararge aegeria*). *Anim. Behav.* **31**, 1206–1216.

Windig, J. J. 1998 Evolutionary genetics of fluctuating asymmetry in the peacock butterfly (*Inachis io*). *Heredity* **80**, 382–392.

Windig, J. J. 1999 Trade-offs between melanization, development time and adult size in *Inachis io* and *Araschnia levana* (Lepidoptera: Nymphalidae)? *Heredity* **82**, 57–68.