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SEXUAL DIMORPHISM IN WING CELL PATTERNS IN *XANTHOCNEMIS ZEALANDICA* McLACHLAN (ZYGOPTERA: COENAGRIONIDAE)

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In many odon. spp. ♂♂ and ♀♀ differ phenotypically; the most commonly noticed characters which exhibit sexual dimorphism are size, and body- and wing colouration. Although the odon. wing venation has been studied intensively, very limited data on sexual dimorphism exist. In this study distinct cell groups in the wings of *X. zealandica* were compared between ♂♂ and ♀♀. Of the 6 cell groups studied two were sexually dimorphic. Reasons for the observed differences are discussed.

INTRODUCTION

Sexual dimorphism is a well known phenomenon in the animal kingdom and is widespread in insects. In dragonflies sexual dimorphism in size has been explored in some detail (e.g. ANHOLT et al., 1991; CROWLEY & JOHANSSON, 2002). However, the most easily noticed forms of sexual dimorphism in this order are body- and wing colouration (e.g. *Crocothemis annulata*, *Calopteryx splendens*). The odonate wing venation and wing-cell patterns have been studied extensively. Most studies have focused on systematics (e.g. MAIBACH, 1986; TRUEMAN,1996) and on fluctuating asymmetry (e.g. RAHMEL & RUF, 1994; HARDERSEN, 2000). A number of studies have also analysed wing morphology in relation to aerodynamics (e.g. GORB, 1999) and flight performance (TAYLOR & MERRIAM, 1995).

Studies on sexual dimorphism in the wing venation of insects are sparse (e.g. COWLEY et al., 1986; VILORIA et al., 2003) and appear not to have been analysed adequately in Odonata. PETERS (1989) and DE JONG (1999) provide data on this subject, without however showing sexual dimorphism in wing-cell

patterns. Some other papers touch on this subject, without addressing if wing-cell patterns differ between males and females. MAIBACH (1986) found a number of differences in cell numbers between males and females in the genus *Calopteryx*, but did not analyse the data for this aspect. TAYLOR & MERRIAM (1995) provided data on sexual dimorphism in wing morphology (length and width) in *Calopteryx maculata*.

In an analysis of fluctuating asymmetry in the wings of *Xanthocnemis zealandica*, HARDERSEN (2000) had to exclude certain cells from the analysis when combining the data from males and females because he found that males and females of *X. zealandica* differed in cell numbers. In contrast, RAHMEL & RUF (1994) reported no such differences for the same cell-group between male and female *Coenagrion puella*, although it is unclear it they tested for such differences.

This paper analyses the data of HARDERSEN (2000) for sexual dimorphism and discusses the results in relation to behaviour and evolution.

MATERIAL AND METHODS

The material and methods are described in detail in HARDERSEN (2000). For the analysis presented here only the animals from the controls in that study were used. A brief summary of the material and methods is as follows:

Larvae of *X. zealandica* were collected on 13 and 14 November 1995 from "The Groynes" (43°27'S, 172°36'E), a recreational area north of Christchurch, New Zealand. On 15 November 1995, 30 morphologically intact larvae which had a head width of 3.0-3.5 mm (putative instar 13) were allocated to each of 5 glass aquaria (4,5 l). A stainless steel mesh (2.5 mm squares, size ca. 700 cm²) served as a perch for the larvae. An air-pump oxygenated the water and kept it in motion. The larvae were provided with superabundant food (mainly *Daphnia* spp.). The aquaria were fitted with mesh caps at the start of the experiment to retain emerging damselflies. The caps were checked every second day. Adults were removed and stored individually in labelled Eppendorf tubes filled with 70% ethanol.

Damselfly fore- and hindwings were cut off and placed on microscope slides. A coverslip was positioned over the wing and fastened with glycerine. Each slide was analysed using a Burle video camera (High resolution CCD) equipped with a Micro-Nikkor lens (55mm/1:2.8). The image was displayed on a TV monitor together with lines created by a For-a video micro scaler (IV 550), so that the length of wings (basal end of basal antenodal cell to the tip of wing; Fig. 1) could be measured. The cell numbers of three distinct areas were counted:

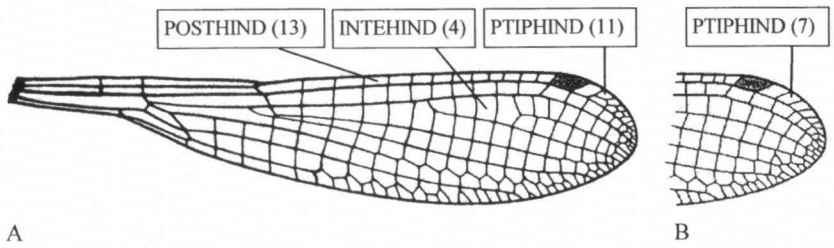


Fig. 1. Hindwings of *Xanthocnemis zealandica* (A: male, B: female partially) with the areas indicated in which cells were counted. The figures in parentheses give the number of cells in the wings shown.

- single cells at the joint of radius 2 and radius 3 (INTEFORE/INTEHIND),
- postnodal cells (POSTFORE/POSTHIND)
- cells between the costa and the radius between the pterostigma and the tip of the wing (PTIPFORE/PTIPHIND)

The data were analysed using the statistical package of Microsoft Excel 2000 (Version 9.0.3821 SR-1). The appropriate t-test (assuming equal variances or assuming unequal variances) was chosen, based on the results of an f-test.

RESULTS

A total of 143 damselflies emerged, equalling 95,3% emergence success. This figure indicates that the conditions were suitable for the maintenance of larvae of *X. zealandica.*

The analysis of the characters of the wings and the comparisons of females and males are summarized in Table I. The wings of females were 8,1% (forewing) to 8,2% (hindwing) larger than those of males ($P < 0.001$ in both cases). Furthermore, the variance was significantly greater for females for both wings. The number of INTEFORE and INTEHIND cells did not differ significantly. Females had a small (0,34 cells in forewing, 0,32 cells in hindwing) but significant higher number of POSTFORE and POSTHIND cells. In contrast, the number of PTPFORE and PTIPHIND cells was markedly and significantly higher in males. In the forewing males had on average 0.67 cells more than females. In the hindwings the difference was much more pronounced, with males having on average 2,23 more cells in the apical region of the hindwing than females. Interestingly the variance for the number of cells in PTPFORE and PTIPHIND between females and males was highly significant ($P < 0,001$), with the spread of the distribution significantly greater in males (Figs 2-3).

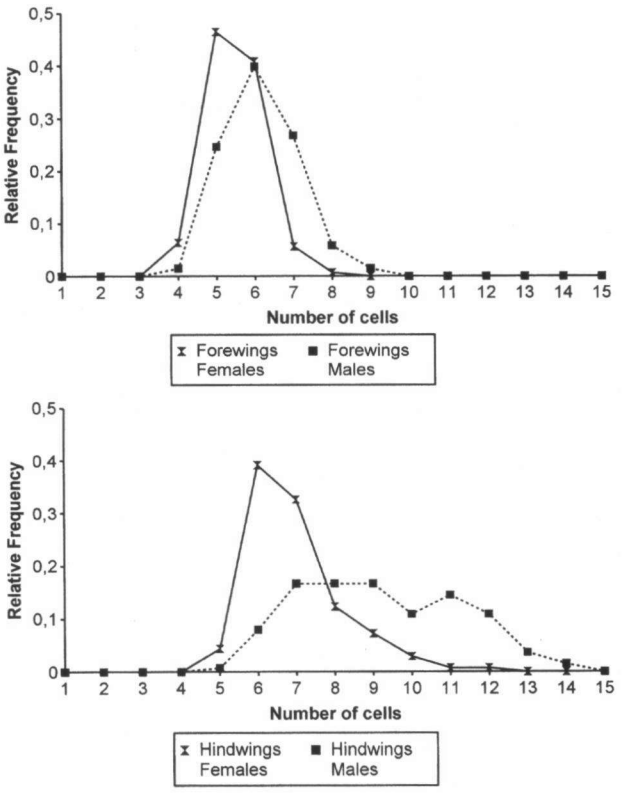
Table 1
Comparisons of characters of the wings

Area	Females		Males		Comparisons	
	Average	Variance	Average	Variance	Variance (f-test)	Mean (t-test)
LENGFORE	190,50	40,25	176,21	26,43	0.007	< 0,001
LENGHIND	180,12	37,71	166,45	23,90	0.004	< 0,001
INTEFORE	3,86	0,50	3,85	0,42	0,14	0,89
INTEHIND	4,29	0,38	4,17	0,33	0,21	0,09
POSTFORE	14,72	1,14	14,38	1,00	0,21	0.006
POSTHIND	12,61	0,67	12,29	0,89	0.048	0.003
PTIPFORE	5,48	0,54	6,15	0,92	<0,001	<0,001
PTIPHIND	6,94	1,54	9,17	4,28	<0,001	<0,001

DISCUSSION

As in many other coenagrionid species, females of *X. zealandica* were found to have a greater wing-length than males (e.g. CONCI & NIELSEN, 1956; LAJEUNESSE & FORBES, 2003). The difference in size between females and males was approximately 8% in the current study, thus *X. zealandica* is sexually dimorphic in size, since the reference-value considered to classify a species as sexually dimorphic is 5% (CUERVO & MØLLER, 1999). This conclusion most probably also holds true for weight and thorax length because it has been shown that wing length is correlated with weight (BRODIN & JOHANSSON, 2002) and thorax length (JOHANSSON, 2003) in the family Coenagrionidae.

One wing area (INTEFORE and INTEHIND) did not show any statitical differences between females and males in the wings analysed. This central part of fore- and hindwing is presumably of high importance to aerodynamic functionality of the wing and therefore biomechanical constraints cause high phenotypic stability.



Figs 2-3. Distribution of cell-numbers in: (2) "PTPFORE" of the forewing; – (3) "PTPHIND" of the hindwing.

Another wing area (POSTFORE and POSTHIND) was consistently larger in females. The slightly difference in cell numbers between genders measured only ca 2,5% and is thus not considered sexually dimorphic. It can probably be explained by allometry. In other words; a longer wing has more postnodal cells.

In contrast, the numbers of cells between the pterostigma and the tip of the wing were consistently higher in males, a difference

which cannot be explained by allometry. This sexual dimorphism has to have another explanation than purely a scaling relationship because the smaller sex showed a larger number of cells between the pterostigma and the tip of the wing in both the fore (12%) and the hind (32%) wings (PTPFORE and PTIPHIND). To my knowledge this is the first time that sexual dimorphism has been shown to occur in the wing venation of dragonflies.

Another aspect to note is that the number of cells between the pterostigma and the tip of the wing showed a pronounced difference between front- and hind-wing, particularly in males (49.1%). In females it was 26.6% , whereas In none of the other cell numbers analysed did it exceed 18%. Moreover, the variance (as a measure of spread) was much larger in PTIPHIND of males in comparison with females, another statistical feature of wing pattern in dragonfly wings that has not been reported before. DE JONG (1999) suggested that the number of cells analysed by him varied more in females than in males. However analysis of his data revealed no statistical difference (t-test, $p > 0,3$).

Wing morphology of dragonflies has been shown to react in subtle ways to shifts in selective forces (e.g. TAYLOR & MERRIAM, 1995). What might be the reason for this partial sexual dimorphism in wing cell patterns in *X. zealandica*, which seems to be particularly noticeable in the cells between the pterostigma and the tip of the wing? Here theoretical aspects of sexual dimorphism have to be considered to arrive at a hypothesis.

In many cases sexual selection drives morphological differentiation between the sexes. However, natural selection can also be responsible for sexually dimorphic characters. To elucidate a possible explanation for the observed differences in the characters PTPFORE and PTIPHIND it is thus necessary to consider arguments for the mode of selection.

It has been shown that traits which are costly to produce or maintain can provide an honest signal for male quality (e.g. GRETHER, 1997) and are sexually selected. Typically, traits under directional sexual selection show high phenotypic variance (ANDERSSON, 1994). The number of PTIPHIND cells in males does show much higher variance than in females. However, to be sexually selected the trait size (e.g. cell number) has to be easily recognized by females. Although damselflies are highly visual animals, they seem to me unlikely to notice an increase in cell-numbers at the tip of the wing, particularly, because no courtship is known to exist in this species (ROWE, 1987). Males do however use their wings for aggressive wing warning (CRUMPTON, 1975; ROWE, 1987). In conclusion, it seems unlikely that sexual selection has acted on the characters PTIPHIND (and to a lesser degree on PTPFORE) and caused an increase in the number of these cells as a signal for mate quality. This conclusion is supported by the fact that no correlation was found between male size (often found to be an indicator of high fitness in male Odonata, e.g. SOKOLOVSKA et al., 2000) and the number of cells (data not shown).

Therefore, the sexual dimorphism in the cells between the pterostigma and the tip of the wing is more likely to have evolved by natural selection involving flight requirements or other mechanical functions (e.g. resistance against wear) which are confined to the male sex. Behavioural differences between males and females are to a large degree differences in reproductive behaviour. Males in the South Island of New Zealand commonly swarm. In most instances several males pursue one female (ROWE, 1987). They also chase each other in aerial contests (Crumpton, 1975, pers. obs.). Although CRUMPTON (1975) states that "on no occasion was bodily contact seen", it seems likely that swarming and aerial contests could result in some physical contact, particularly involving the tips of the wings. However, if aggressive male-male interaction was the main cause of the observed differences, it is not clear why the cell numbers should be higher in the hindwings.

Another occasion where mechanical strain in the wing tips of males is likely to occur is during copulation. While in tandem male wings are likely to touch the female at least occasionally. For example, figure 3c in CRUMPTON (1975) shows a tandem of *X. zealandica* where the wings almost touch the head of the female. Moreover, when the wings are folded over the body the hindwings protrude much more than the frontwings. Thus it is obvious that contact with the female would almost exclusively occur in the hindwings. In order to resist such mechanical strain the tips of the hindwings should be more resistant to wear. Therefore it is possible that physical contact with the female while in tandem is the main reason for the increased cell number in PTIPHIND in *X. zealandica*, a morphological feature which most likely provides increased resistance to wear (see Fig. 1).

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