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OPEN AND BANDED WINGS: HYPOTHESES ON DAMSELFLY WING POSITION (ZYGOPTERA)

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Zygoptera spp. either perch with their wings open or closed. The alternatives do not appear to be phylogenetically constrained, as there are sexual differences in *Ecchlorolestes peringueyi*, and population variation and individual variation in *Pseudagrion sublacteum*. Open wings would appear to be more conspicuous to predators (Shiny Wing Hypothesis). Yet there is a difference between clear and coloured, banded wings in *Chlorolestes* spp. Clear wings appear to be associated with crypsis, either in open or forest habitats. For spp. that have banded wings (and banded bodies), those individuals that are banded are aggressively territorial to clear-winged conspecifics and are sexually more attractive to ♀♀. Open-winged perching behaviour is associated with perching on tips of shoots and rapid escape from ground predators, supporting the Quick Takeoff Hypothesis. Conspicuous open-winged perching for banded-wing individuals appears to be a tradeoff between territorial superiority on the one hand and predation from aerial predators, particularly birds, on the other. Predation however, appears to be minor relative to the advantages gained by conspicuousness.

INTRODUCTION

Within the Zygoptera, there is a dichotomy between those species, genera or families that perch with their wings along their abdomen and the minority that perch with their wings open. PAULSON (2004) proposes a hypothesis that the open-wing position facilitates either more rapid takeoff or quicker orientation toward flying prey: *The Quick Takeoff Hypothesis (QTH)*. The evolutionary tradeoff would be increased vulnerability to predators when wings are spread: *The Shiny Wing Hypothesis (SWH)*.

The South African odonate fauna comprises two open-wing families (Synlesti-

dae and Lestidae) and the rest with wings closed. These open-wing species occur in a range of habitat complexity from open to closed canopy. This range of variation, which includes apparent balanced polymorphism of wing coloration, provides further evidence to accept or reject PAULSON's (2004) hypotheses, and is investigated here.

FURTHER EVIDENCE

SEXUAL DIFFERENCES

PAULSON (2004) indicates that no sexual differences in wing position have been reported. There is however, one synlestid species, *Ecchlorolestes peringueyi* (Ris, 1921), where the male has remarkably clear wings and perches, wings outstretched on lichen-covered boulders (Figs 1-2). In contrast, the female, which has slightly smoky wings, particularly at the tips, perches with closed wings (Fig. 3). She perches on twigs, as well as on boulders.

INDIVIDUAL DIFFERENCES

Pseudagrion sublacteum (Karsch, 1893) normally perches with wings closed (Fig. 4). However, certain populations of *P. sublacteum* have male individuals that perch with wings partially open (Fig. 5). Females in the same population also do so (Fig. 6). During tandem mating, the males maintain partially open wings (Fig. 7). This species may also have other wing positions, including differences on each side (Fig. 8), and occasionally with completely open wings (Fig. 9).

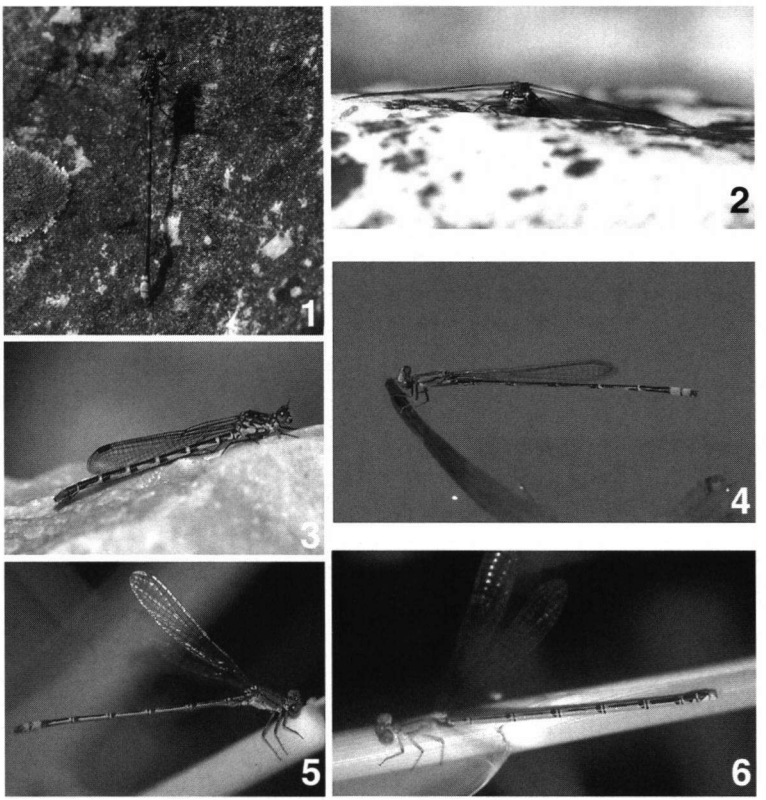
WING PATTERNING

All South African closed-wing species have clear or slightly smoky wings. They never only have coloured wing banding. All seven South African *Lestes* species perch with wings open and do not display. Six of the seven are open habitat species, generally seeking shade only as tenerals or when alarmed. The only species that occurs under closed canopy (and not always) is *L. virgatus* (Burmeister, 1839), and it has smoky wings. The other six spp. have clear wings.

Ecchlorolestes nylephtha (Barnard, 1937) and *E. peringueyi* have clear, open wings. Unlike open-habitat *E. peringueyi*, *E. nylephtha* inhabits distinctly closed canopy with a minimum of sunflecks. The seven *Chlorolestes* species all perch with wings open, and some male individuals when sexually mature have heavy black and white wing bands (Tab. I), which is usually associated with heavy, whitish body pruinescence, particularly in *C. umbratus* Hagen *in* Selys, 1862 (Fig. 10). Some individuals in some populations never develop wing banding. All agonistic encounters between banded and unbanded *C. fasciatus* (Burmeister, 1839) result

in the unbanded male being chased away by the banded male.

All male individuals of some *Chlorolestes* species have clear wings and are never banded (*C. conspicuus* Hagen *in* Selys, 1862 and *C. draconicus* Balinsky, 1956). Both are essentially open-canopy species (Tab. I). Of the banded wing species [*C. apricans* Wilmot 1975, *C. fasciatus*, *C. tessellatus* (Burmeister, 1839) and *C. umbratus*], certain entire populations of *C. fasciatus*, *C. tessellatus* and *C. umbratus* have only clear wings. The entirely clear-winged populations of *C. fasciatus* and *C. umbratus* are inhabitants of more closed canopy than is usual for the species.



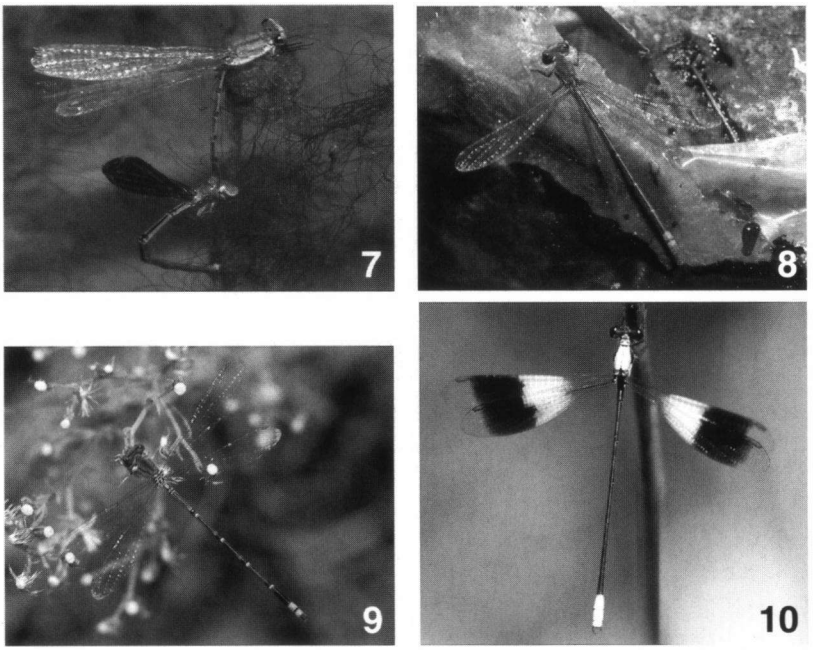
Figs 1-6. Wing positions and colouring in some South African Zygoptera: (1) ♂ *Ecchlorolestes peringueyi* perching with very clear open wings, and highly cryptic, on a lichen-covered boulder (Bainskloof, Western Cape Province, May 1993); – (2) ♂ *E. peringueyi* perching, front view, showing low gomphid-like profile (Bainskloof, Western Cape Province, May 1993); – (3) ♀ *E. peringueyi* perching on boulder, but with slightly smoky, closed wings along the abdomen (Bainskloof, Western Cape Province, May 1993; – (4) ♂ *Pseudagrion sublacteum* perching with wings closed (Otto's Bluff, KwaZulu-Natal Province, February 1996); – (5) ♂ *P. sublacteum* perching with partially open wings (Thumbu, Umfolozi, KwaZulu-Natal Province, February 1991; – (6) ♀ *P. sublacteum* from same population with partially open wings (Thumbu, Umfolozi, KwaZulu-Natal Province, February 1991).

Although PINHEY (1951) records an individual of *C. elegans* Pinhey, 1950 with banded wings. Not one has been recorded since.

C. tessellatus is generally banded in the Eastern Cape Province but rarely banded farther north. The only banded male recorded from KwaZulu-Natal in recent years was weakly banded and was present in a habitat much more open than is normal for the species.

DISCUSSION

The banded-wing condition is only associated with open-wing species, and then only certain individuals, populations or species of *Chlorolestes*. None of the other open-wing genera, *Ecchlorolestes* and *Lestes*, are banded. The banded-wing condition is also associated with very strong agonistic behaviour, with banded--winged individuals vigorously chasing away conspecific clear-winged individuals. Furthermore, there is a weak tendency within a species for banded-wings to be



Figs 7-10. Wing positions and colouring in some African Zygoptera, continued: (7) Mating pair of *Pseudagrion sublacteum*, with ♂ maintaining partially open wings, even while clasping ♀ (Valley of a Thousand Hills, KwaZulu-Natal Province, May 1996); – (8) ♂ *P. sublacteum* perching with wings on eitherside held in different positions (Mayotte, Comoros, June 2001); – (9) ♂ *P. sublacteum* perching with wings held in the fully open position (Keate's Drift, KwaZulu-Natal Province, April 1999); – (10) banded ♂ *Chlorolestes umbratus* perching conspicuously, with wings open.

Table I
Wing banding and habitat choice in South African *Chlorolestes* spp.

Species	Habitat		
	Closed canopy	Partially closed	Open
Chlorolestes apricans	-	-	B/C
C. conspicuus	-	C	C
C. draconicus	-	C	C
C. elegans	C/B	C/B	-
C. fasciatus	-	B/C	B/C
C. tessellatus (WCP)	-	C	-
" (ECP)	B	B	-
" (KZNP)	C	C	C/PB
C. umbratus	B/C	B	-

WCP = Western Cape Province, ECP = Eastern Cape Province, KZNP = KwaZulu-Natal Province; B = banded wings, C = clear wings, PB = partially banded; - = not recorded and probably not applicable.

associated with more open canopy conditions. Where banded-winged individuals occur in forest (e.g. *C. tessellatus* in the Eastern Cape Province, and *C. umbratus* in the Southern Cape), they are strongly associated with sunflecks and are strongly territorial. Sunfleck-associated territoriality has been recorded for both temperate (WATANABE et al., 1987) and tropical (ORR, 2004) zygopterans.

The banded-winged individuals are remarkably conspicuous and presumably vulnerable to aerial predators. There seems to be a tradeoff between conspicuousness (risk from predation) and territoriality. Interestingly, two distinctly forest species, *Ecchlorolestes nylephtha* and *Lestes virgatus* have slightly and very smoky wings respectively, and both are very well camouflaged. *E. nylephtha* in particular, as other South African synlestids to a lesser extent, engages in characteristic up-and-down waving of its pale, pruinescent abdomen tip. This may possibly send a signal to potential predators that there is the possibility of a sting (which there is not of course). Certainly, in *C. tessellatus*, females are more likely to mate with banded males than unbanded ones (K.L. Pringle, pers. comm.), so it may be that the waving is more a sexual signal than a warning to predators.

These results support to some extent PAULSON's (2004) (*QTH*). *Chlorolestes* perch very exposed on the tips of bushes. They do not hide as do many closed-wing coenagrionids (MILLER, 1995) but instantly take off when alarmed. It is not known whether this behaviour has benefits for breeding, but certainly does not refute this suggestion.

These South African synlestids are an unusual assemblage in that none of the other members of the family (from Asia, Australia and Hispaniola) show banded wings, although most of them perch with the wings open at least some of the time (PAULSON, 2004 and pers. comm.). These South African species are also

unusual in that some of them live in the open, while the other, non-South African synlestid species, all seem to be associated with forest streams, lending further support to bandedness being largely associated with open conditions

The *Predator Avoidance Hypothesis* (*PAH*), which is embedded in the *QTH*, is supported by *E. peringueyi.* The male has open wings and is exceptionally cryptic, even in its very exposed microhabitat. It can as rapidly take flight from the surface as a gomphid. Yet the slightly smoky-winged female has closed wings. But she maintains her versatility, because as well as being camouflaged on rocks, she also perches on twigs and oviposits there.

As a corollary, predator avoidance is a relative term according to realities. The adult South African synlestids are virtually immune to attack by fish, amphibians, reptiles and non-flying mammals as they perch on shoot tips at least 50 cm (and usually much more) up and over the water. The minutest vibration causes them to take flight. Not one has ever been seen to be captured by an anisopteran. Indeed, *Anax speratus* Hagen, 1867, the most likely candidate for predator, as it is large and cruises along mountain streams, flies right past perching *Chlorolestes* species. Furthermore, no synlestid has ever been recorded in a spider's web, although it is not uncommon to record other zygopterans trapped in webs in the same locality. The most likely predators are birds, but there is no obvious insectivorous bird in the synlested habitats that would take damselfly prey of this particular size. Indeed, no wing remains after bird attack have ever been discovered. One possibility as predators in some areas could be bee-eaters (Meropidae) but the host and potential predator are only marginally sympatric.

The *Phylogenetic Inertia Hypothesis* (*PIH*), which states that wing position is constrained by phylogenetic pedigree (HEYMER, 1975) is not borne out here. The evidence from *P. sublacteum* is that there can be remarkable intraspecific variation in wing position. Furthermore, PAULSON's (2004) point, quoting from V. Clausnitzer, that high-elevation *Pseudagrion* species perch with wings partially open, while lowland spp. hold them closed, is also not supported here. All the high-elevation South African *Pseudagrion* species hold their wings tightly closed and behave cryptically when disturbed. *P. sublacteum* is a low to moderate elevation spp. (< 700 m a.s.l.).

In conclusion, PAULSON's (2004) *QTH* is supported, but quick takeoff may be not just for feeding but also for territorial defense. The evidence, however, for predator avoidance is equivocal. For the open-winged and clear-winged synlestids, predator avoidance may come about by being cryptic, either as dark green forest species or marbled brown rock-sitting species. Other individuals of many, but not all, species appear to go to the other extreme and are highly apparent, with banded wings and whitish pruinescence Although it is not known whether this is aposematic, it is certainly associated with territorial defense and enhanced sexual acceptance. Bird predation, it seems, in these cool stream habitats is minimal and worth risking for enhanced intraspecific dominance.

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