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Openwing perching in some Zygoptera (Odonata): a response to Klaus Reinhardt

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Abstract

Herein I respond to a critique of my paper on wing positions in Zygoptera. The author of that critique suggested that most of the hypotheses presented in that paper were flawed and questioned some of the facts brought to bear on them. In addition, he presented his own ideas in support of hypotheses I had rejected. I take this opportunity to clarify my reasoning further. Although I did not elaborate sufficiently in some cases, no statement made in my paper was incorrect. My critic and I are in agreement that this is a complicated matter, and all hypotheses continue to be worth further testing.

Introduction

Reinhardt (2006), hereafter Reinhardt, writing about the hypotheses presented in my paper on wing positions in Zygoptera (Paulson 2004), stated "A critical examination suggests that most of them have substantial flaws that prevent their testing." As this is a serious criticism, I will attempt to respond to his critique, at the same time taking advantage of the opportunity to add additional information that I had not considered essential to the first paper. The criticisms are sufficiently detailed that my responses will have to be similarly detailed. I follow the headings of Reinhardt's paper.

At the outset, I should reiterate that my primary goal in writing this paper was to raise the question of the adaptive significance of different wing positions in zygopterans, and in Odonata in general. Rather than merely making suggestions about fruitful research directions, I generated a series of formal hypotheses and tried to marshal evidence to support or refute them. My conclusions, interestingly, were the same as those of Reinhardt: that we need more research and more data. In no way did I intend to present the picture that the questions had been answered, but I believe hypothesis testing is the way to answer them.

Definitions

Reinhardt concluded that "erecting and testing hypotheses regarding the origin and maintenance of OWP requires tighter definitions than those provided by Paulson." He began by criticizing my definitions of openwing position (OWP). I stated that to be considered an openwing species, it must perch with wings spread nearly or completely to the horizontal, at least some of the time. Reinhardt stated "it is unclear whether Paulson did classify the openwing roosting by calopterygids as OWP in his paper." In fact, Table 1 in my paper makes it clear which genera I classified as OWP, and I did not include any calopterygid. My definition should have been made more clear that "some of the time" was intended to mean a behavior of regular occurrence during the day's activities, but I believed that odonatologists on every continent would have a clear picture of OWP vs CWP species. I made it clear that I was not including coenagrionids that perched with wings half-open as OWP species, notwithstanding Reinhardt's admonition that they should be so categorized. I do not agree that "in the Coenagrionidae it is very difficult to decide whether a wing position is open or half-open," nor in the Lestidae, as he further states. Besides my 45 years of experience watching odonates, I looked at many hundreds of photos while preparing the 2004 paper and found nothing to shake my confidence that typical wing positions could be assigned to each species. Of course many individual odonates hold their wings in positions not typical from time to time. I have photos of several coenagrionids that opened their wings as I watched them and held them that way for more than a few seconds, but I do not consider such behavior in a CWP species as significant in the context of my hypotheses. Apparently relatively few species (genera listed in my table 1) are consistent in using both open and closed modes during normal activity.

As I did not define perching, I am also surprised that Reinhardt criticized my definition of it. Again, this is an activity that needs no definition for it to be clearly understood by anyone who observes animals that fly. When they are not flying, they are perched. He stated that several activities I cited as examples of instances when *Lestes* close their wings "do not appear to fall under the category 'perching'," but nowhere did I call these activities perching. In fact, they had nothing to do with perching vs flying, only citing all situations outlined by Jödicke (1997) in which *Lestes* closed their wings. To me, the obvious point of this statement was that *Lestes* normally kept their wings open when perched but that they could be closed in a variety of circumstances.

Phylogenetic Inertia Hypothesis

First, I assumed it was clear that I attempted to bring three explanations proposed in the literature to explain wing position into the realm of modern science and therefore treated them as hypotheses from which predictions could be made.

Reinhardt stated, with regard to the phylogenetic inertia hypothesis, "the lack of a phylogenetic approach and a lack of testable predictions makes Paulson's rejection of this hypothesis invalid." Indeed I did not specify a prediction stemming from this hypothesis, although I think the information presented was sufficient for readers to draw their own conclusions. In retrospect I should have stated clearly that this hypothesis would predict that either OWP or CWP would occur in only a limited number of zygopteran clades, depending upon which was ancestral, but that both would not be widespread in the suborder. Instead, both are known in all three zygopteran superfamilies, and, exactly as Reinhardt pointed out, a substantial number (five or six) of shifts in perching position would have had to occur within the Zygoptera no matter the ancestral state. The phylogeny of Rehn (2003) shows a slightly different picture than that of Bechly (1998), but wing position varies in a similar number of clades. Thus wing position seems not to have been phylogenetically constrained over the evolutionary history of the Zygoptera. Furthermore, although I was remiss in not quantifying the number of CWP genera in families that included OWP genera, I should add that in at least five families, both OWP and CWP genera occur, and even within genera, both modes may be used (table 1 in the earlier paper). Thus the character seems to be evolutionarily labile even at present.

Wing Display Hypothesis

Reinhardt stated "The suggestion that OWP is related to wing display requires that wing display does occur from a perch. This assumption was not tested." My reason for including this hypothesis was, as stated, Heymer's (1975) discussion of wing display in euphaeids, in which *Epallage fatime* (Charpentier) displayed with closed wings and *Dysphaea dimidiata* Selys with open wings while perched. I agree with Reinhardt that many odonates practice flight displays, but I considered exactly what Heymer claimed, that closed wings can be used for display as well. To the eyes of a male *Calopteryx*, another male is surely a conspicuous territory holder even though it is entirely stationary. This is quite rightfully called a display, just as when a male *Anolis* lizard extends its colorful dewlap and holds it in position.

I should have explicitly stated a third prediction that I thought was implicit, that if OWP evolved for display, then it should be characteristic of more species with colored wings, as the colors are surely important in display. In any case, at our present state of knowledge, most species that are known to display with their wings perch with them closed. As Reinhardt claimed, it is difficult to assign any observed pattern to the perching position, but, as I claimed, Heymer's hypothesis that wing position is related to wing display has no support.

Quick Takeoff Hypothesis

I ascribed an advantage of OWP to the Zygoptera because almost all Anisoptera utilize it. Reinhardt's response is that "this argument is not compelling because OWP in the Anisoptera is likely to originate from a single evolutionary event." I agree entirely, but the fact that the genera *Cordulephya* and *Zenithoptera* represent two independent switches to the CWP mode, as I pointed out, indicates a lack of phylogenetic constraint, at least in the Libelluloidea. All anisopterans have their wings closed when they finish their emergence and then open them, so there is nothing about being an anisopteran that precludes closed wings, and I think it is productive to look for an ecological or behavioral explanation of the uniformity in the suborder, just as it is similarly productive to try to explain the variation in Zygoptera.

Reinhardt criticized my basic prediction for this hypothesis that OWP species should be salliers and CWP species should be gleaners. Instead, he suggested that I should have predicted that sallying species should exhibit OWP more often than gleaners. I agree with his logic entirely, but the prediction was stated as it was because we know much about wing position but almost nothing about foraging behavior. My thought was that I would work from the known to the unknown, as befits a hypothetico-deductive approach. Nevertheless, salliers do exhibit OWP more than gleaners (table 3 of my paper; *Pseudagrion* indeed was included in both foraging categories), and a two-tailed Fisher's exact probability = 0.003 as before. Reinhardt also questioned my lack of explanation of how takeoff time was measured in a species of *Lestes* (OWP) and a species of *Ischnura* (CWP). Individuals (25 *Lestes disjunctus* Selys and 43 *Ischnura cervula* Selys) were watched with a video camera until they took off from their perch spontaneously (causes for takeoff varied). The takeoff was filmed, and takeoff time was defined as the amount of time it took the animal to move one body length off the perch, thus adjusting for size. The mean takeoff time of the *Lestes* (0.092 s) was significantly shorter than that of the *Ischnura* (0.116 s) ($p = .0057$). Reinhardt stated that the time between takeoff and actual prey capture would be more relevant than takeoff time itself, but the QTH predicted only a faster takeoff time for OWP species, which was confirmed. I stated that this difference needed to be further tested, and indeed between species as closely related as possible. I suggest a good test would be comparisons of Australian lestids, which include OWP (*Lestes*) and CWP (*Austrolestes*) genera that Rehn (2003) considered members of the same clade.

Reinhardt also questioned the list of genera in my table 2. First, he notes that "39% of the genera are from a single family, the Coenagrionidae, for which OWP likely represents only one evolutionary event." I assume he meant wing position, as OWP does not characterize the family. If only family level is considered, there is still a strong association between open wings and sallying and between closed wings and gleaning. Excluding Lestidae, which are OWP and CWP salliers, and Coenagrionidae, which are CWP gleaners and salliers, four families exhibit OWP and sallying and three families exhibit CWP and gleaning. Only two families exhibit the less-expected association between CWP and sallying; see below for a discussion of the Calopterygidae, one of these exceptions. The sample of genera for that table was very small, as stated at the time, but it included at least half of the approximately 20 zygopteran families, and I eagerly await research on wing positions and foraging methods in other families that I hope this paper will stimulate. Notwithstanding the fact that the categorization of 20 out of 35 genera was based solely on my own observations, it is quite incorrect that any of them disagree with the published record. *Lestes* species do indeed capture some of their prey by gleaning, as Jödicke (1997) pointed out, but sallying is much more common than gleaning in that genus (R. Jödicke pers. comm.). As I wrote earlier, my student J.A. Scales (unpubl.) found that *L. disjunctus* fed by sallying about 90% of the time ($n = 381$ prey-capture attempts), and from my own observations, I consider that typical of the genus. I also wrote that *I. cervula* foraged by gleaning 75% of the time ($n = 847$). From Scales' study and my many hours of watching these and other species of their genera, I think it is appropriate to classify *Lestes* as a sallier and *Ischnura* as a gleaner. We do not consider swallows gleaners just because they pick up insects from the ground at times. Furthermore, neither I nor anyone else, to my knowledge, has written that calopterygids were openwing species, based on the definition given above, nor that they forage by any means other than sallying. Where is the disagreement?

Further, Reinhardt found two examples "counter to Paulson's observations: *Mortonagrion* and *Platycnemis* employ midair foraging." In fact, it was not clear that the dominant mode of foraging in these two CWP genera was sallying, as concluded by Reinhardt from a table in Corbet (1999: 356). The authors of both of the papers cited by Corbet merely discuss "feeding flights" and capture success but make no mention of what proportion of the flights were directed toward flying vs stationary prey. Because of this, I did not include them in my table 2. I have subsequently learned that *Mortonagrion hirosei* Asahina and *M. selenion* (Ris) capture prey by both sallying and gleaning (not quantified), while *Platycnemis echigoana* Asahina appears to be entirely a sallier (M. Watanabe pers. comm.).

An important point that I neglected to make in my paper is that gleaning zygopterans do not hesitate to capture prey in flight, as they often flush insects they attempt to capture from the substrate. Thus gleaners regularly employ midair foraging, but they are already in flight when they do so and thus do not have to employ a rapid takeoff. The rarity of observations on foraging zygopterans surely contributed to the absence of this fact from Corbet (1999).

Shiny Wing Hypothesis

Reinhardt pointed out, with regard to my statement that OWP species were typically large zygopterans, that my "supporting table 1 does not contain measurements of wing or body size." This omission was purposeful, as for such measurements to be meaningful, I would have had to furnish an average or range of measurements for each genus, as the list was of genera and not species. Furthermore, I would have had to furnish similar measurements for comparison of all the CWP genera, a huge list, and neither editor nor reviewers asked for that unreasonable amount of effort. I assumed readers would either know the world fauna well enough or accept my word that the OWP genera are among the larger zygopterans.

Reinhardt, in response to my assumption that zygopterans would be subject to a greater variety of predators than anisopterans because they are smaller, stated "there is no obvious theoretical reason why predation risk should be related to the number of predator species." In fact, I consider it a basic ecological principle that smaller species should have both more kinds of predators and more individual predators than larger ones. The reason for this was put succinctly by Hutchinson & MacArthur (1959: 117): "If we examine the fauna of any area we find that the groups containing the largest numbers of species are for the most part groups of small animals, whereas large animals are represented mainly by genera containing a few species. This is in part doubtless an expression of the Eltonian pyramid of numbers and sizes; there will usually be few species of groups in which there are few individuals ..." Larger animals are not only less common than their prey but also less diverse than smaller ones in virtually all taxa (for birds and mammals, see Maurer et al. 1992). Thus the smaller the animal, the more species and individuals of potential predators it should have – no matter what its predators. I see this as increased predation risk. For example, zygopterans should have predators, either arthropod or vertebrate, that are too small to eat anisopterans, yet the larger predators that can handle anisopterans are well-equipped to capture and eat the smaller zygopterans as well.

Reinhardt: "Paulson then neglects his predicted relationship between conspicuousness and wing holding within the Zygoptera because he compares all Zygoptera against all Anisoptera, not just their OWP representatives: 'odonate collectors know that Anisoptera are harder to catch than Zygoptera.'" My logic would maintain that OWP zygopterans are part of the larger class of all zygopterans, and thus the statement is entirely reasonable. Perhaps Reinhardt misunderstood the point I was trying to make, that our own observations tell us that zygopterans in general are more vulnerable to predation than anisopterans, and thus there may be stronger selective pressure on zygopterans not to be conspicuous by open wings. Having no data on the comparative foraging success of falcons, swallows, bee-eaters and odonates on zygopterans and anisopterans, I used the best information available, the response of odonates to an approaching insect net.

Reinhardt: "Other supportive observations by Paulson are irrelevant to the Shiny Wing Hypothesis: the avoidance of male sexual approaches by females ... the relationship between OWP and the maturation period ... or whether the abdomen is held below or between the wings." In fact, the first two of these are entirely relevant to that hypothesis. I presented anecdotal evidence that individuals closed their wings in situations that might represent either potential predation or potential harassment of females by conspecific males. It is straightforward to conclude that open wings are more conspicuous than closed wings, especially from above. The point about the maturation period is that although *Lestes* commonly perch in the sun while at the water, at least some of them spend more of their life in the shade than in the sun, so they furnish no evidence against the claim that OWP species are shade-lovers. Finally, my comments about whether the wings were held over the abdomen or alongside it in certain coenagrionids were in the discussion and not in reference to a particular hypothesis. However, this information is relevant to any assessment of correlations of wing position and foraging, as I noted that sallying coenagrionids were more likely to hold the wings raised, gleaning genera more likely to hold them along the abdomen. Although I was merely calling attention to this behavioral dichotomy, it seems reasonable to me that the difference in wing position could relate to the quicker takeoff that I still claim would be a valuable adaptation for a sallying species.

I should further comment that to me it still makes sense that if zygopteran wings are held closed to avoid detection by predators that may be above them, then this selective pressure might cause any group with brightly colored wings, often broad ones (Calopterygidae, Chlorocyphidae, Euphaeidae, Polythoridae), to hold them closed. Furthermore, they may also be more effective in display to conspecifics when closed because such individuals are likely to approach from the side, not from above or below. This hypothesis, like others I have erected informally, is subject to field testing.

Thermoregulation Hypothesis

Although I have no bias against any hypotheses to explain zygopteran wing positions, I have seen no evidence yet to convince me that thermoregulation plays a significant part. The few examples given by Corbet (1999: 287, 317) of zygopterans using their wings as reflectors or heat trappers are not compelling as explanations of the CWP that is so prevalent in zygopterans.

Reinhardt stated "Paulson ... did not consider Miller's (1995: 25) suggestion that warm air trapped under the lowered wings may keep the thorax temperature high and thus allow rapid flight." Firstly, Miller's suggestion was directed toward anisopterans that hold their wings considerably depressed while perching; the zygopterans I wrote about hold their wings slightly above the horizontal, and I see no way they would trap warm air beneath them. Secondly, I argued that most OWP species were shade-dwellers, and they would have no sun-warmed air or sun-warmed thorax to make this an effective strategy. May's (1976) paper on a libellulid tested the effect of wings shading the thorax, unlikely in a zygopteran because of its narrow wing bases. Because of this, I find Reinhardt's statement that "heat gain by OWP in the Zygoptera at cool temperatures would be the opposite effect of body cooling (if any) by thorax shading as found in the Anisoptera" puzzling.

Finally, I question Reinhardt's suggestion that "in sun-perchers CWP may assist in avoiding overheating ...". The wings of a zygopteran cannot shade its thorax, because of their typical perching positions and the skewness of the zygopteran thorax. The wings might shade the abdomen if closed, but only if they are held directly between the sun and the abdomen, and I have not seen evidence that zygopteran perching positions change during the course of the day in any way that would bring the wings into play to accomplish ectothermal thermoregulation.

Conclusion

There are so many instances in which my hypotheses and the evidence supporting them were inconclusively criticized by Reinhardt that I was left with the feeling of frustration that we could be so far apart in our thinking. Perhaps "misunderstanding" would better define the situation. He admonished finally that researchers should not accept my hypotheses and should not consider my "tests as valid rejections of previously existing ideas." I concur wholeheartedly with the spirit of that statement as a request for further study rather than an attempt to discredit my evidence, and I encourage others to continue to test all of the hypotheses presented in my paper. We need much more information about foraging by and predation on adult odonates, for example. My statements of both support and rejection were based on the evidence available to me, and I stand by them. But I would hope that in the future new information will be acquired that will allow us to understand the selective pressures that bring about the different wing positions in perching Odonata. A fruitful avenue of research would surely be to study species that appear to vary in their wing positions during normal activity (I listed *Rimanella*, *Euphaea*, *Episynlestes*, *Synlestes*, and *Chorismagrion* as genera in which this occurs) to understand the context of this variation (M.L. May pers. comm.). I must add that I am not the first to contemplate zygopterans with open wings. To quote Tillyard (1917: 323), "*Diphlebia* and *Argiolestes*, however, resemble the Gomphinae in their method of rest. They sit on rocks, sand or twigs, with wings horizontally poised for flight. From such a position they move off very rapidly."

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Erratum

In Paulson (2004: 509), *Philoganga* was inadvertently listed twice in table 1. It should be deleted from the Amphipterygidae.