Received 20 May 2003; revised and accepted 06 April 2004

Why do some zygopterans (Odonata) perch with open wings?

Dennis R. Paulson
Slater Museum of Natural History, University of Puget Sound, Tacoma, WA 98416, USA. <dpaulson@ups.edu>

Key words: Odonata, dragonfly, Zygoptera, behavior, foraging, flight.

Abstract

Zygoptera show two perching modes, one with wings closed and one with wings open. These perching modes are distributed unequally through the suborder; most Zygoptera perch with closed wings, but species in 43 genera of eight families at least occasionally – in most cases usually – perch with open wings. Alternative hypotheses to explain this dichotomy are assessed. The dichotomy does not seem to be explicable by the Phylogenetic Inertia Hypothesis (PIH), the Wing Display Hypothesis (WDH), or the Thermoregulation Hypothesis (TH). I propose a hypothesis that the openwing position used by some zygopterans facilitates either more rapid takeoff or quicker orientation toward flying prey: the Quick Takeoff Hypothesis (QTH). That openwing species usually take flying prey furnishes support for the QTH, although many closedwing species also take flying prey. However, as most zygopterans perch with closed wings, that behavior needs explanation too, and I propose a hypothesis that perching with wings spread may make a zygopteran more conspicuous to predators and thus may be disadvantageous: the Shiny Wing Hypothesis (SWH). Larger species are less at risk of predation than smaller species, open wings in shade should be less conspicuous than in sunlight, and the majority of zygopterans with open wings are large tropical shade perchers, furnishing support for the SWH.

Introduction

One of the features used to distinguish Zygoptera from Anisoptera is that most zygopterans perch with their wings closed over their abdomen, while almost all anisopterans perch with them held open. Thus it is of some interest that certain zygopterans, typically at the family or genus level (Table 1), perch with wings outspread, as in anisopterans. The total of 43 genera of eight families that are known to perch in this manner is minimal, as other genera in some of the included families are very likely to perch with open wings. The incomplete knowledge of this phenomenon is indicated by Corbet's (1999: 287) listing of only 11 genera of five families in this category. However, the Lestidae, Synlestidae, and Megapodagrionidae are families with substantial diversity that comprise primarily openwing species.

I call these two modes 'openwing' and 'closedwing' perching and the zygopterans that use them openwing and closedwing species, respectively. To qualify for openwing status, the species must perch with wings spread nearly or completely to the horizontal, at least some of the time. Some species apparently alternate open and closed positions. Some zygopterans of the family Coenagrionidae – e.g., *Chromagrion conditum* (Hagen), *Coenagrion hastulatum* (Charpentier) – habitually perch with the wings about half-open, well above the horizontal plane, and I do not consider them in this discussion. Openwing species typically hold their wings from slightly above the horizontal plane to horizontally as in anisopterans, although tilted backwards because of a different thoracic angle. Only one species deviates from this, the euphaeid *Dysphaea dimidiata* Selys that may depress its fore wings as much as 40° and hind wings as much as 30° below the horizontal (Paulson 1981a).

Hypotheses

Explanations of the significance and function of two modes of wing position in the Zygoptera have been surprisingly few, considering the dichotomy would have been apparent as soon as odonate studies began in Europe. No explicit hypotheses have been posed and tested, but three explanations have been proposed in the literature, and I propose two additional ones.

Phylogenetic Inertia Hypothesis (PIH)

Heymer (1975) proposed a phylogenetic explanation for the open wings of *Epallage fatime* Charpentier (Euphaeidae), but it lacked cohesion. He remarked on its similarity to another euphaeid, *Dysphaea dimidiata*, to other 'primitive' zygopterans *Philoganga* (Amphipterygidae) and *Argiolestes* (Megapodagrionidae), and to anisopterans such as *Orthetrum*. But he did not tie these groups together phylogenetically, and he did not attempt to explain why other genera of these zygopteran families perched with wings closed. A corollary of this hypothesis is that wing position may be a non-adaptive expression of an ancestral condition.

Wing Display Hypothesis (WDH)

Heymer (1975) also noted that the wings of *E. fatime* were closed in display, and he proposed that the open wings of *D. dimidiata* also functioned in display (independently proposed by Paulson 1981a). Paulson (1981b) proposed that wings may be broader in species of several families with colored wings (Amphipterygidae, Polythoridae, Euphaeidae, Calopterygidae, Pseudostigmatidae) in order to function more effectively in display. Predictions that can be made from this hypothesis include (1) at least some openwing species should use their wings for display, and (2) displays are more likely in males than females, so there should be sexual differences in wing position.

Thermoregulation Hypothesis (TH)

Jacobs (1955) suggested that anisopterans lowered their wings at high temperatures to shade their thorax; thus wing position has an effect on thermoregulation. Corbet (1999: 287) suggested that different wing positions might relate to ectothermic thermoregulation but took the idea no further. He cited reports of calopterygids that roosted with spread wings during inclement weather, perhaps for thermoregulatory advantage.

Quick Takeoff Hypothesis (QTH)

The openwing position must be advantageous to odonates, as almost all Anisoptera utilize it. Assuming there is an advantage to the openwing position in Zygoptera as well, I chose to focus on some aspect of flight behavior that might be affected by it. My hypothesis is that openwing zygopterans either have a quicker takeoff than closedwing species or are able to orient more quickly in their intended flight direction and that this would correlate with some aspect of their foraging, escape, or reproductive behavior. For example, with a quicker takeoff and/or quicker orientation, a zygopteran could respond more quickly to approaching predators, prey, or conspecifics. All openwing species hold their wings at or slightly above the horizontal (*D. dimidiata* the lone exception) and separated from one another and should thus be able to benefit by a quick downward wingbeat.

Looking only at foraging behavior, the QTH assumes that sit-and-wait foragers that take flying prey ('salliers') would benefit by a quicker takeoff time, while those zygopterans that forage by hover-gleaning off the substrate while in flight ('gleaners') would not have been under such strong selection for rapid takeoff. The hypothesis thus predicts (1) faster takeoff times in openwing than in closedwing zygopterans and (2) that openwing species will typically forage by sallying, closedwing species by gleaning.

Shiny Wing Hypothesis (SWH)

Assuming a flight advantage in the openwing position, what selection might there be against that position in zygopterans, even in those that forage by sallying? If resting with wings open is advantageous, then why don't all zygopterans do so? As virtually all anisopterans and some zygopterans perch with open wings, no one has yet asked the obvious question "why do most zygopterans perch with closed wings?" I hypothesize that wings, although transparent, are likely to reflect sunlight and therefore make their bearer more conspicuous to predators. Thus even if the openwing position were advantageous, the necessity to remain cryptic to potential predators might have exerted sufficient selective pressure to cause most zygopterans to perch with wings closed.

Two predictions can be made from the SWH relating wing position to both size and habitat. First, smaller species should be more at risk from predators, and closed wings should therefore be more common in smaller species. Zygopterans are

smaller than anisopterans, on average, so I assume they are more subject to predation by a greater diversity of predators, although no data are available to verify this assumption. It is common knowledge among odonate collectors that anisopterans are harder to capture than zygopterans, so zygopterans that are conspicuous because of wing position may be at greater risk from aerial predators than anisopterans that are conspicuous for the same reason; anisopterans have a greater chance of escaping a predation attempt. In fact, a basic prediction of this hypothesis is that Anisoptera would perch with open wings and Zygoptera with closed wings, as is the case.

Second, habitat should influence wing position. Because wings are more conspicuous when they reflect sunlight (D. Paulson pers. obs.), the SWH also predicts that zygopterans that usually perch in the shade are more likely to use the openwing position than those that usually perch in the sun.

Evidence

Phylogenetic Inertia Hypothesis

Wing position is at least somewhat associated with phylogeny in zygopterans, because open wings occur in some families but not others. In addition, wing position characterizes genera; they are almost all either entirely openwing or entirely closedwing; the only exception known to me is *Euphaea* (P. Goffart and M. Hämäläinen pers. comm.). However, as the ancestral zygopteran presumably perched in only one of these two modes, and both modes are scattered through the Zygoptera, they presumably arose independently in more than one of the three superfamilies Calopterygoidea, Lestinoidea, and Coenagrionoidea. Thus an adaptive explanation for both positions is to be sought, whether or not it applies to all species now using them. The wing position of numerous tropical genera has not been reported, so it is impossible at present to determine the proportion of genera in each family that perches openwing. However, because openwing and closedwing genera are found in at least five zygopteran families (Amphipterygidae, Euphaeidae, Lestidae, Synlestidae, Megapodagrionidae; D. Paulson unpubl.), I reject this hypothesis.

Wing Display Hypothesis

As zygopterans that use their wings in display for the most part have colored wings (poorly documented but known especially in Calopterygidae and Chlorocyphidae), and the majority of openwing zygopterans have uncolored wings (D. Paulson unpubl.), there is no apparent correlation between open wings and wing displays. Of course, many closedwing zygopterans with both colored and uncolored wings open them in response to disturbance (Corbet 1999: 471). Wing display is poorly documented in odonates, but I know of no openwing zygopteran with uncolored wings that uses its wings for display. Furthermore, no sexual differences in wing position in odonates have been reported. I reject this hypothesis.

Table 1. Zygopterans known to perch with open wings. Published photos, if not obviously posed, are considered as representing at least one incidence of perching style. *: species of genus and/or individuals of species may perch with open or closed wings.

Family	Genus	Source
Amphipterygidae[1]	*Philoganga*	Kemp & Butler (2001)
	*Rimanella**	T. Donnelly pers. comm.
Diphlebiidae	*Diphlebia*	D. Paulson pers. obs.; Plate IIIb
	Philoganga	Photos in Wilson (1995) and Silsby (2001)
Dicteriadidae	*Heliocharis*	Paulson (1981a)
Euphaeidae	*Anisopleura*	M. Hämäläinen pers. comm.
	Dysphaea	Lieftinck (1959), Paulson (1981a)
	Epallage	Heymer (1975)
	*Euphaea**	P. Goffart and M. Hämäläinen pers. comm.
Synlestidae	*Chlorolestes*	D. Paulson pers. obs.
	*Chorismagrion**	Silsby (2001); G. Theischinger and R. Rowe pers. comm.
	Ecchlorolestes	Photos in Samways (1995) and Silsby (2001)
	*Episynlestes**	D. Paulson pers. obs.
	Megalestes	Photos in Hämäläinen & Pinratana (1999) and Silsby (2001)
	Sinolestes	K. Wilson pers. comm.
	*Synlestes**	D. Paulson pers. obs.
Lestidae	*Archilestes*	Paulson (1981a)
	Lestes	Described by many authors
	Orolestes	Photos in Hämäläinen & Pinratana (1999) and Silsby (2001)
	Platylestes	Fraser (1933); Paulson (1981a)
	Sinhalestes	de Fonseka (2000)
Megapodagrionidae	*Amanipodagrion*	Clausnitzer (2003)
	Archiargiolestes	Watson et al. (1991)
	Argiolestes	T. Donnelly and R. Rowe pers. comm.; photo in Silsby (2001)
	Austroargiolestes	D. Paulson pers. obs.
	Celebargiolestes	J. van Tol pers. comm.
	Dimeragrion	Photo in De Marmels (1989)
	Griseargiolestes	D. Paulson pers. obs.; Plate IIIa
	Heteragrion	Paulson (1981a)
	Hypolestes	Needham (1941)
	Miniargiolestes	Watson et al. (1991)
	Oxystigma	J. De Marmels pers. comm.
	Philogenia	Paulson (1981a)
	Philosina	Photos in Wilson (1999)
	Podolestes	Paulson (1981a)
	Podopteryx	R. Rowe pers. comm.; photo in Silsby (2001)
	Pseudolestes	K. Wilson pers. comm.
	Rhinagrion	Paulson (1981a)
	Rhipidolestes	Photos in Ishida et al. (1988) and Silsby (2001)
	Sciotropis	J. De Marmels pers. comm.
	Teinopodagrion	D. Paulson pers. obs.
	Trineuragrion	Photo in Silsby (2001)
Perilestidae	*Perissolestes*	D. Paulson pers. obs.

[1] *Amphipteryx* was listed erroneously as openwing by Paulson (1981a).

Thermoregulation Hypothesis

Wings are held differently at different ambient temperatures, but the use of wing position to accomplish thermoregulation has not been clearly shown except by May (1976), who found that wing position in the libellulid *Pachydiplax longipennis* (Burmeister) influenced thoracic temperature. However, he could not confirm that lowering the wings (shading the thorax) acted to lower body temperature, as proposed by Jacobs (1955). Ectothermic thermoregulation in odonates is accomplished in the sun; thus, if open wings were involved in thermoregulation, they should occur in zygopterans that normally perch in the sun. For the most part, this is not the case (see below). Furthermore, the calopterygids mentioned by Corbet (1999: 318) that roosted in openwing position at night usually closed their wings before the rays of the sun reached them. I reject this hypothesis.

Quick Takeoff Hypothesis

The evidence to support the QTH is sparse, but there is no robust evidence against it. For the first prediction of faster takeoff time in openwing species, a study of takeoff time quantified on videotape (J.A. Scales unpubl.) compared two species, *Lestes disjunctus* Selys and *Ischnura cervula* Selys. *L. disjunctus* perches with wings open and forages primarily by sallying (about 90% of prey-capture attempts). *I. cervula* perches with wings closed and forages primarily by gleaning (about 75% of prey-capture attempts). The former species had a significantly faster takeoff time as indicated by analysis of video frames of numerous takeoffs by each species. This sample hints at a difference that needs further confirmation by comparisons of takeoff times among additional species.

Surprisingly few foraging studies are available to test the second prediction relating open wings to sallying (Table 2). Many of the entries in this table are from my own observations, often of just a few individuals, but I consider them representative until better-quantified studies appear. Openwing genera so far studied all forage by sallying, while closedwing genera may be salliers or gleaners (Table 3). This is unfortunately a very small sample of the 272 genera of Zygoptera, and well-chosen foraging studies would add much to present knowledge. It is of interest, however, that only one of the two types of foraging behavior characterizes most families, with only the Coenagrionidae definitely including both types.

Shiny Wing Hypothesis

Looking at the first prediction made by the SWH, relating size to wing position, openwing genera tend to be relatively large and robust zygopterans (Table 1), presumably with fewer predators than their smaller relatives. The zygopteran families with the smallest species (Platystictidae, Platycnemididae, Coenagrionidae, Protoneuridae, Isostictidae) are conspicuously absent from the list. Interestingly, only two genera of Anisoptera regularly perch with closed wings: the corduliid *Cordulephya* (Watson et al. 1991) and the libellulid *Zenithoptera* (Paulson 1981). Both contain species that are quite small for their family, and *Zenithoptera* has brilliantly colored, conspicuous upper wing surfaces that are hidden when the wings are closed.

Table 2. List of zygopteran genera for which wing position and foraging type are known.

Family	Genus	Wing position	Foraging type	Foraging reference
Diphlebiidae	*Diphlebia*	open	sallier	D. Paulson pers. obs.
	Philoganga	open	sallier	K. Wilson pers. comm.
Calopterygidae	*Calopteryx*	closed	sallier	D. Paulson pers. obs
	Hetaerina	closed	sallier	D. Paulson pers. obs.
	Mnais	closed	sallier	Higashi et al. (1979)
	Mnesarete	closed	sallier	D. Paulson pers. obs.
	Phaon	closed	sallier	O'Neill & Paulson (2001)
Dicteriadidae	*Heliocharis*	open	sallier	D. Paulson pers. obs.
Synlestidae	*Synlestes*	open	sallier	D. Paulson pers. obs.
Lestidae	*Archilestes*	open	sallier	D. Paulson pers. obs.
	Austrolestes	closed	sallier	R. Rowe pers. comm.
	Lestes	open	sallier	D. Paulson pers. obs.
	Sympecma	closed	sallier	R. Jödicke pers. comm.
Megapodagrionidae	*Austroargiolestes*	open	sallier	D. Paulson pers. obs.
	Heteragrion	open	sallier	Shelly (1982)
Coenagrionidae	*Acanthagrion*	closed	gleaner	D. Paulson pers. obs.
	Aeolagrion	closed	sallier	D. Paulson pers. obs.
	Apanisagrion	closed	gleaner	D. Paulson pers. obs.
	Argia	closed	sallier	Shelly (1982)
	Austroagrion	closed	gleaner	D. Paulson pers. obs.
	Chrysobasis	closed	gleaner	D. Paulson pers. obs.
	Enallagma	closed	gleaner	D. Paulson pers. obs.
	Hesperagrion	closed	gleaner	D. Paulson pers. obs.
	Ischnura	closed	gleaner	D. Paulson pers. obs.
	Leptobasis	closed	gleaner	D. Paulson pers. obs.
	Metaleptobasis	closed	gleaner	D. Paulson pers. obs.
	Pseudagrion	closed	gleaner[1]	Corbet (1962); Meskin (1986)
	Teinobasis	closed	gleaner	V. Clausnitzer ms
	Xanthocnemis	closed	gleaner	Rowe (1987)
Isostictidae	*Rhadinosticta*	closed	gleaner	D. Paulson pers. obs.
Platystictidae	*Protosticta*	closed	sallier	K. Wilson pers. comm.
Protoneuridae	*Psaironeura*	closed	gleaner	S. Pairis pers. comm.
Pseudostigmatidae	*Coryphagrion*	closed	gleaner	Clausnitzer & Lindeboom (2002)
	Megaloprepus	closed	gleaner	Fincke (1992)
	Pseudostigma	closed	gleaner	Fincke (1992)

[1] *Pseudagrion* has been seen to feed by both methods.

There are numerous exceptions to the relationship between large size and open wings in zygopterans. Interestingly, these large, closedwing species of the families Polythoridae, Euphaeidae, Calopterygidae, and Pseudostigmatidae have colored and patterned wings, and open patterned wings might be as conspicuous as open sunlit wings. Thus as exceptions they offer support to the hypothesis.

The second prediction, relating habitat to wing position, is supported by the differences in the two sallying species studied by Shelly (1982). The openwing *Heteragrion erythrogastrum* Selys typically perches in the shade, the closedwing *Argia difficilis* Selys in the sun, consistent with the hypothesis. Additionally, it is noteworthy that of the 43 genera in Table 1, all but one are tropical or subtropical, and most are shade perchers (D. Paulson pers. obs.), a strategy more feasible in the warm tropics than at higher latitudes, where sun perching may be essential to activity. Of the genera on this list, only *Lestes* is common and widespread at high latitudes. Many species of *Lestes,* both tropical and temperate, perch in the sun while at the water, but during their lengthy maturation period (as long as three months; Corbet 1999: 301), most of the species occur in shady woodland. I should add that watching *Lestes* at the water, their wings brilliantly reflecting sunlight, first led me to consider this hypothesis.

Discussion

In the suborder Zygoptera there are dichotomies in both wing position and foraging behavior and loose but seemingly significant associations among these variables. The QTH cannot be rejected, although additional research is needed to support it more clearly. The SWH is supported by the preponderance of large, shade-loving species among openwing genera.

If open wings make their bearer more conspicuous to predators, then such species might close their wings when predators appeared. Three anecdotal observations support this prediction: (1) a *Lestes viridis* (Vander Linden) closed its wings each time a patrolling *Aeshna cyanea* (O.F. Müller) approached it within about 0.5 m (M. Wasscher pers. comm.); (2) *L. vidua* Hagen closed its wings whenever an anisopteran – usually *Erythemis simplicicollis* (Say), a predator on other odonates – came near (Dunkle 1990); (3) Utzeri et al. (1987) reported that females of *L. barbarus* (Fabricius) and *L. virens* (Charpentier) close their wings when approached by *Aeshna* or *Sympetrum*. In addition, females might close their wings to be less conspicuous to avoid harassment by conspecific males. Female *L. barbarus* closed their wings when approached by conspecific males (Utzeri et al. 1987), and unpaired ovipositing female *L. sponsa* (Hansemann) closed their wings when patrolling males of the same species approached (R. Stoks pers. comm.). Jödicke (1997) listed five situations in which *Lestes* rest with closed wings: (1) the first minutes after emergence (pp. 174, 198), (2) dying and dead individuals (pp. 198, 246), (3) during submerged oviposition (p. 236), (4) during low temperatures (p. 206), and (5) unpaired females during oviposition when approached by males (p. 218). Clearly these animals are able to modify their wing position and thus must "choose" to hold them open, but I have no such information about the many other zygopterans with open wings.

Besides inconspicuousness, might there be other advantages in the closedwing position? Some insects are thought to generate lift by a special mechanism called "clap-and-fling" flight, in which useful air circulation around the wings is created when the wings are suddenly opened (Weis-Fogh 1976). This was described for a

Table 3. Zygopteran wing positions vs foraging types. All openwing genera are salliers, while closedwing genera are more likely to be gleaners. Two-tailed Fisher's exact probability = 0.003; n = 36 genera.

	Sallier	Gleaner
Openwing	8	0
Closedwing	10	18

butterfly and a fly, and no one has analyzed odonate flight in this context, but if rapid opening of the wings does produce enhanced lift, this could be another reason for zygopterans perching with their wings closed. However, recent high-speed videos taken by R. Beckemeyer and watched by the author show that at least some coenagrionids appear to open their wings before they use them for flight. When approached by an observer, *Megaloprepus caerulatus* (Drury) typically opened their wings partway, presumably in preparation for taking flight, and then if left alone, would close them again (O. Fincke pers. comm.).

Further study of closedwing coenagrionid species will be of value, as they show interesting variation. For example, high-elevation species of *Pseudagrion* (e.g., *P. bicoerulans* Martin) in East Africa perch with wings partially open, while lowland species hold them closed (V. Clausnitzer pers. comm.); is this evidence for a thermoregulatory function? This might be tested on more accessible species of *Coenagrion* or *Chromagrion*. Another difference can be found even in genera in which the wings are held tightly closed. Species of the genus *Argia*, which are known to be salliers, always perch with their wings elevated slightly above their abdomen, while those of *Ischnura* and *Enallagma*, typical gleaning species, perch with their wings alongside their abdomen (Manolis 2003; D. Paulson pers. obs.). The difference is obvious in photographs. Other genera of the Coenagrionidae appear to follow this dichotomy, species of a given genus perching either in one way or the other. I speculate that even this small difference might indicate a difference in takeoff speed or other aspects of flight responsiveness, and studies of foraging in coenagrionids should take note of this characteristic.

In addition, from photos I have examined, it is evident that numerous species of calopterygids (at least in the genera *Calopteryx* and *Hetaerina)* perch with the wings either held on one side of the abdomen or elevated well above it, perhaps the latter a position of greater readiness to fly; this is another hypothesis that could be tested. Tiefenbrunner (1990) found that in *Sympecma fusca* (Vander Linden), the wings were held on the side of the abdomen opposite a heat source (sunlight or lamp) but on the side of the heat source at higher temperature, indicating a thermoregulatory function for this behavior; holding the wings above the abdomen still needs explanation. The variation in wing position in both closedwing and openwing species is worthy of further consideration.

Acknowledgements

For information about wing positions, foraging behavior, and pertinent references, I am grateful to Viola Clausnitzer, Philip Corbet, Jürg De Marmels, Nick Donnelly, Sid Dunkle, Philippe Goffart, Matti Hämäläinen, George Harp, Rodolfo Novelo-Gutiérrez, Samantha Pairis, Richard Rowe, Tom Schultz, Robby Stoks, David Thompson, Antoine van der Heijden, Nancy van der Poorten, Jan van Tol, Marcel Wasscher, and Keith Wilson. Thanks to Jeff Scales for information on takeoff times of zygopterans, to Ola Fincke for comments on the manuscript, and to Roy Beckemeyer for suggesting I consider clap-and-fling flight and for a very informative video of Odonata in flight. I thank also Andreas Martens and Michael May, who carefully reviewed this paper and improved it greatly.

References

Clausnitzer, V., 2003. Rediscovery of *Amanipodagrion gilliesi*, with notes on habitat, behaviour and conservation (Odonata: Megapodagrionidae). International Journal of Odonatology 6: 1-8.

Clausnitzer, V. & M. Lindeboom, 2002. Natural history and description of the dendrolimnetic larva of *Coryphagrion grandis* (Odonata). International Journal of Odonatology 5: 29-44.

Corbet, P.S., 1962. A biology of dragonflies. H.F. & G. Witherby Ltd., London.

Corbet, P.S., 1999. Dragonflies: behavior and ecology of Odonata. Cornell University Press, Ithaca.

de Fonseka, T., 2000. The dragonflies of Sri Lanka. WHT Publications (Private) Limited, Colombo.

De Marmels, J., 1989. Odonata or dragonflies from Cerro de la Neblina. Academia de Ciencias Físicas, Matemáticas y Naturales, Caracas 25: 1-91.

Dunkle, S.W., 1990. Damselflies of Florida, Bermuda and the Bahamas. Scientific Publishers, Gainesville.

Fincke, O.M., 1992. Behavioral ecology of the giant damselflies (Odonata: Zygoptera: Pseudostigmatidae) of Barro Colorado Island, Panama. In: Quintero, D. & A. Aiello (eds) "Insects of Panama and Mesoamerica, selected studies", Oxford University Press, Oxford, pp. 102-113.

Fraser, F.C., 1933. The fauna of British India, including Ceylon and Burma, Vol. I. Taylor & Francis, London.

Hämäläinen, M. & A. Pinratana, 1999. Atlas of the dragonflies of Thailand – distribution maps by province. Brothers of St. Gabriel in Thailand, Bangkok.

Heymer, A., 1975. Der stammesgeschichtliche Aussagewert des Verhaltens der Libelle *Epallage fatime* Charp. 1840. Zeitschrift für Tierpschologie 37: 163-181.

Higashi, K., S. Nomakuchi, Y. Okame & T. Yasuda, 1979. Daily food consumption of *Mnais pruinosa* Selys (Zygoptera: Calopterygidae). Odonatologica 8: 159-169.

Ishida, S., K. Ishida, K. Kozima & M. Sugimura, 1988. Illustrated guide for identification of the Japanese Odonata. Tokai University Press, Tokyo. [In Japanese; English title].

Jacobs, M. E. 1955. Studies on territorialism and sexual selection in dragonflies. Ecology 36: 566-586.

Jödicke, R., 1997. Die Binsenjungfern und Winterlibellen Europas. Lestidae. Westarp, Magdeburg.

Kemp, R.G. & S.G. Butler, 2001. Some dragonfly records from Phewa Tal, Pokhara, Nepal, with notes on *Philoganga montana* (Selys) (Zygoptera: Amphipterygidae). Notulae Odonatologicae 5: 88-91.

Lieftinck, M.A. 1959. Waterjuffers voor de lens. De Levende Natuur 62: 98-106.

Manolis, T., 2003. Dragonflies and damselflies of California. University of California Press, Berkeley.

May, M.L. 1976. Thermoregulation and adaptation to temperature in dragonflies (Odonata: Anisoptera). Ecological Monographs 46: 1-32.

Meskin, I., 1986. Territorial behaviour in *Pseudagrion hageni tropicanum* Pinhey (Zygoptera: Coenagrionidae). Odonatologica 15: 157-167.

Needham, J.G., 1941. Life history notes on some West Indian coenagrionine dragonflies (Odonata). Journal of Agriculture of the University of Puerto Rico 25: 1-18.

O'Neill, G. & D.R. Paulson, 2001. An annotated list of Odonata collected in Ghana in 1997, a checklist of Ghana Odonata, and comments on West African odonate biodiversity and biogeography. Odonatologica 30: 67-86.

Paulson, D.R., 1981a. Peculiar wing position in *Dysphaea dimidiata* Selys (Zygoptera: Euphaeidae). Notulae Odonatologicae 1: 134-135.

Paulson, D.R., 1981b. Anatomical modifications for displaying bright coloration in megapodagrionid and chlorocyphid dragonflies (Zygoptera). Odonatologica 10: 301-310.

Rowe, R., 1987. The dragonflies of New Zealand. Auckland University Press, Auckland.

Samways, M.J., 1995. Conservation of the threatened, endemic dragonflies of South Africa. In: Corbet, P.S., S.W. Dunkle & H. Ubukata (eds) "Proceedings of the international symposium on conservation of dragonflies and their habitats," Japanese Society for Preservation of Birds, Kushiro, pp. vii, 8-15.

Shelly, T.E., 1982. Comparative foraging behavior of light- versus shade-seeking adult damselflies in a lowland neotropical forest (Odonata: Zygoptera). Physiological Zoology 55: 335-343.

Silsby, J., 2001. Dragonflies of the world. Smithsonian Institution Press, Washington.

Tiefenbrunner, W., 1990. *Sympecma fusca* (Vander Linden, 1820): Korrelation zwischen Flügelstellung und Lichteinfallswinkel in Abhängigkeit von der Temperatur (Zygoptera: Lestidae). Libellula 9: 121-132.

Utzeri, C., E. Falchetti & R. Raffi, 1987. Adult behaviour of *Lestes barbarus* (Fabricius) and *L. virens* (Charpentier) (Zygoptera, Lestidae). Fragmenta Entomologica, Roma 20: 1-22.

Watson, J.A.L., G. Theischinger & H.M. Abbey, 1991. The Australian dragonflies. CSIRO, Canberra & Melbourne.

Weis-Fogh, T., 1976. Energetics and aerodynamics of flapping flight: a synthesis. Insect Flight, Symposia Royal Entomological Society of London 7: 48-72.

Wilson, K.D.P., 1995. Hong Kong dragonflies. Urban Council of Hong Kong, Hong Kong.

Wilson, K.D.P., 1999. Dragonflies (Odonata) of Dinghu Shan Biosphere Reserve, Guangdong Province, China. International Journal of Odonatology 2: 23-53.