Fliers and perchers among Odonata: dichotomy or multidimensional continuum? A provisional reappraisal

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ABSTRACT

We revisit the hypothesis, first advanced in 1962, that, with regard to their means of thermoregulation and overt behaviour, two types of Odonata can be recognised: fliers, when active (during reproductive activity, primarily, or foraging) remain on the wing, whereas perchers, when similarly engaged, spend most of the time on a perch from which they make short flights. First, in light of the available data, we restrict the hypothesis to apply primarily to activity at the rendezvous. Next, we review evidence, including direct measurements of body temperature coupled with activity budgets, to test the proposition that the hypothetical classification constitutes a dichotomy rather than a continuum. We conclude: (1) that there is merit in retaining the dichotomous classification into fliers and perchers, together with the thermoregulatory capabilities assigned to each category; (2) that the distinction between fliers and perchers is sufficiently discrete to be a useful predictor of the suite of thermoregulatory strategies and energy demands characteristic of representatives of each category; and (3) that, within each category a continuum exists such that the capacity to heat the body by irradiation (i.e. ectothermically) or by metabolic heat production (endothermy) increases with body size. Some departures from expectation based on the percher/flier dichotomy reflect the increased flight activity that occurs at the rendezvous under conditions of heightened conspecific or interspecific interference. Other apparent anomalies are identified as topics for potentially fruitful research.

THE FLIER/PERCHER TEMPLATE

Forty-six years ago Corbet (1962) hypothesised that, with regard to their means of thermoregulation and overt behaviour, two types of Odonata can be recognised. Fliers are those that, when active, remain on the wing, whereas perchers, when active, spend most of their time on a perch from which they make short flights (Corbet 1962). At the time this difference was rationalised in terms of the dragonfly's need to avoid overheating the body, although this reasoning was based on little more than the inference that, by flying persistently, fliers would be tending to maintain the body temperature at a high level unless they possessed some 'special' compensating

device. Since then, largely due to the experiments and direct measurements conducted by, May (1976, 1977, 1980), Heinrich & Casey (1978), Polcyn (1994), and others, much has been discovered about the options for thermoregulation avai-lable to drag-onflies and the correlation between those options and two variables: body size and microhabitat choice. MLM placed these findings in a broader, physio-logical context in later reviews (May 1978, 1979, 1984, 1991) which confirmed a close correspon-dence between flight patterns and methods of thermoregulation.

The evolution of either flier or percher behaviour entails a number of other corre-lates or consequences besides its relation to thermoregulation. One that may be of at least equal importance is the greater rate of metabolic energy expenditure by fliers during active periods. Flight is certainly the most energetically costly activity that dragonflies undertake (May 1995), and this fact requires that fliers either enjoy less total daily activity time than perchers or must acquire energy by feeding for longer daily periods and/or at higher rates of energy intake than perchers. In fact, several studies of reproductive activity of fliers have found that their typical tenure at rendez-vous sites is on the order of 30 min per day (Kaiser 1974, 1982; Ubukata 1975) while many perchers spend several hours at mating sites. This generalization must be tempered, of course, by the fact that fliers are highly mobile, and in most cases the possibility that they divide their time among several rendezvous sites cannot be entirely excluded. Moreover, although perchers are known to return to sites over periods of 10-62 days (15 species tabulated by Corbet 1999: 651), very few compa-rable data are available for fliers (13-33 days, two species, Corbet 1999: 651).

Fliers commonly exhibit morphological adaptations that tend to ameliorate high energy demands, e.g., longer wings and lower wing loading at a given body mass, with less mass allocated to thoracic muscle and more to fat stores (MLM pers. obs.). These characteristics may imply that fliers, on average, employ less demanding flight maneuvers, although quantitative observations on this point are lacking (May 1989). Marden (1989) showed that in male *Plathemis lydia*, a highly territorial percher, nearly all fat stores are converted to muscle protein, in essence reducing its margin of energetic safety in favour of very high power output. In general, fliers may not be able to make this extreme tradeoff because their routine energy demands make this strategy too risky. Thus we might expect "energetic wars of attrition" (Marden & Waage 1990) to be more likely in perchers, since the energy reserves of the latter are more likely to be exhausted during relatively brief, intense encounters with rivals at the rendezvous. We also note that the manner of flight should have energy conse-quences, although this again has not been examined in dragonflies. Steady flight at moderate speed, as when patrolling an extensive reach of stream, is likely to require lower energy expenditure that very rapid flight, especially when the latter is com-bined with elaborate maneuvering, or very slow flight, e.g., searching for cryptic fe-males along banks of lakes or streams, or hovering. Thus we should expect a number of differences besides the defining one in the time allocation and other aspects of be-haviour between perchers and fliers.

The original definition of fliers and perchers, stated above and used by Corbet (1962, 1980, 1999: 283) has had great heuristic value over the years, but it contains some ambiguity. For example, the definition, and the discussion above, begs the ques-tion of what 'activity' means. Clearly it is not equivalent to either flying or perching per se, although all flight should be included. The question then is, which instances of perching should be considered 'activity' and which should not? Ignoring for the

moment the possibility of truly nocturnal activity, we might take the behaviour at night time roosts as the exemplar of 'inactive perching'. At night and before commencing morning activity, dragonflies typically orient their body axis more or less vertically, in contrast to most 'active' perchers, which orient the body horizontally. At least some species also spend periods of reduced activity, e.g., no sexual activity and little or no feeding, during the day perched either horizontally or more nearly vertically but in very close proximity to conspecifics; e.g. *Brachythemis lacustris* (Kirby) (Miller 1982) and *Sympetrum rubicundulum* (Say) (MLM pers. obs.). Although the habit of perching vertically or in close proximity without interaction may be taken as indicative of 'inactivity', exceptions occur. Males of *Indaeschna grubaueri* (Förster), a species breeding at small pools and large phytotelmata in Southeast Asian tropical rainforest understory, perch in typical vertical aeshnid posture above such sites and mate with females as they arrive. However when feeding, they are semi-crepuscular fliers (Orr 2003). A more accurate indicator of cessation of normal activity, then, is that individuals do not respond, or have at least a much elevated threshold of response, to stimuli that would ordinarily elicit feeding, aggression, or mating attempts; the only class of stimuli to which they are normally responsive are disturbances that might indicate the approach of a predator. We thus suggest that this alteration in responsiveness is the defining criterion for 'activity' and 'inactivity'. Unfortunately, we are unaware of any data beyond anecdote that serve to test the suitability of this criterion or to use it in a rigorous way to define active periods of dragonfly behaviour. Thus we still must rely to a considerable extent on an ill-defined and subjective conception of activity and inactivity. We urge our readers, however, to attempt observations that test our suggested criterion, including exposing presumably inactive dragonflies to model prey items or conspecifics or simply watching such individuals closely for extended periods.

Activity includes at least reproductive activity, foraging, and dispersal, the last sometimes including long-distance migration. Furthermore, it is now clear that, when active, some species in some circumstances fly most but not all of the time. In this paper we explicitly exclude flight during migration, although if, as we contend below, the proposed behavioural dichotomy is closely linked to differences in thermoregulatory strategy and energy requirements, then consideration must be given to the ways in which the demands of maintaining an appropriate body temperature and energy balance can be reconciled with those inherent in migratory behaviour. As a practical necessity we focus largely on reproductive activity because very few data are available for other behaviours. In doing so, however, we do not exclude the possibility that foraging mode (see below) may have an important influence on the evolution of flying vs perching behaviour (D. Paulson pers. comm.).

We also restrict our further attention to Anisoptera on the grounds that data are insufficient to evaluate confidently either perching behaviour or thermoregulation in Zygoptera. We note here, however, that Paulson (2004, and pers. comm.) has documented two foraging modes in Zygoptera, gleaners and salliers, which he associates with predominantly flier and percher behaviour, respectively. Furthermore, although most Zygoptera are probably too small to risk endothermic overheating except in the most extreme conditions, a few, including, e.g., large calopterygids, euphaeids, diphlebiines, and pseudostigmatids may be exceptions. Thus studies of flight behaviour, especially while feeding, and thermal ecology of Zygoptera would repay detailed, extensive and quantitative study.

Even considering only male reproductive behaviour of Anisoptera, a closely typo-logical view of flight behaviour could obscure the full range and diversity of adap-tations to the thermal environment. For example, De Marco et al. (2005), in a statistical analysis of the behaviour/time budget of 10 species of Anisoptera at a lake in southern Brazil (at ca 19°S), concluded that the species fell into three groups. Species in the first and second groups remained perched for at least 75% of the time, the first group (four species) differing from the second in making more transition flights – i.e. flights from one type of activity or microhabitat to another – and, in the case of three species, being more aggressive and spending more time in territorial defence. The second group, containing the four smallest species in the whole assem-blage, rarely defended or patrolled territories. The third group, comprising two species, spent a low proportion of time perched, one of them showing a high pro-portion of patrol flights. According to the conventional classification, the first and second groups would be classed as perchers and the third group as fliers. Those au-thors' main grounds for wishing to qualify the flier/percher classification, based on behaviour were that it did not account adequately for body size and that certain be-havioural measures (e.g. time spent perching) were susceptible to modification de-pending on density at the reproductive site, and the resulting interaction, both within and between species (see Table 1).

In a study of thermoregulatory strategies of dragonflies of Interior Alaska, Sformo & Doak (2006) were able to classify each of the ten species they encountered as a percher or a flier according to its behaviour at the rendezvous, noting that the two categories differed markedly with respect to the thermoregulatory strategies em-ployed. They concluded, nonetheless, that body mass "appears to have a stronger in-fluence on thermal ecology than does behaviour." All the species they classified as perchers were libellulids and all but one were smaller than the species (aeshnids and a corduliid) classified as fliers. The largest percher (*Libellula quadrimaculata* Lin-naeus) and the smallest flier (*Cordulia shurtleffii* Scudder), species of intermediate size, were intermediate also in some of their thermoregulatory attributes but never-theless exhibited the characteristic thermoregulatory traits that correlate securely with each of the two behavioural categories, namely reliance on ectothermic and en-dothermic warming respectively. Their data emphasize the point that smaller Anisoptera generally will thermoregulate relatively poorly (May 1976) and thus must possess adaptations to maintain activity at fairly low temperature. Furthermore, small fliers may be unable to thermoregulate well because forced convection acting on them during flight is higher, relative to the rate of metabolic heat production, than in large fliers. Hence we expect that small Anisoptera will tend to be ectotherms and perchers, at least in cold or temperate habitats.

Having considered carefully the data and arguments presented by De Marco et al. (2005) and Sformo & Doak (2006), we conclude that the flier/percher classification, as modified above and rationalised in terms of the options species have available for thermoregulation, remains robust, and provides an informative template for inter-preting the way in which dragonflies reconcile the demands of thermoregulation and vital processes such as foraging and reproduction. Our basic premise is that, by the inspection of the behaviour of any dragonfly in permissive weather at the rendezvous, it is possible, with few exceptions (amplified below), unequivocally to identify a species as either a flier or a percher. In Table 2 we list the records known to us that are germane to this hypothesis. The Table allows four conclusions: (a) a striking,

Table 1. Strategies for thermoregulation used by active adult Odonata. Source: modified from Corbet (1999: 283).

Strategy	Ambient temperature [1]	
	Low	High
Ectothermic thermoregulation		
Postural adjustment [2]		
Body	– Basking	– Obelisk
Use of wings	– Insulators or solar reflectors	– Parasols for thorax or abdomen
Microhabitat selection		
Sites	– Insolated [3]	– Shaded [4]
Perch level [5]	– Warmer (lower)	– Cooler (higher)
Diel activity pattern		
Time of main activity	– Warmest times of diel	– Coolest times of diel, typically either or both twilights
Reversible, temperature-induced colour change		
Colour phase	– Dark	– Pale
Endothermy		
Metabolic heat generated by flight muscles	– Increase by wing-whirring or flight	– Unload by circulating hemolymph between thorax and abdomen, where it is cooled [6]
		– Reducing amount generated by flight by gliding or reducing wingbeat frequency.
		– Cool by "bathing" or drinking?
		– Evaporative cooling?

[1] In relation to the thoracic temperature permitting spontaneous activity.
[2] Usually when perched; sometimes when flying, when convective cooling can result from airflow across the abdomen; mainly entails positive or negative heliotropism, probably mediated by thermoreceptors in the body wall; sometimes features orientation to wind.
[3] Or, exceptionally, to geothermally warmed sites, e.g. *Rhionaeschna peralta* (Ris) at 4,600 m in the Peruvian Andes (J. Hoffmann pers. comm.; see Corbet 1999: 639).
[4] May include caves or human dwellings.
[5] As the sun rises, the warmest perching sites typically move from the treetops to the ground and vice versa at sunset.
[6] Usually by convection, a process accelerated, especially at higher wind speeds, by airflow across the thorax and abdomen.

quantitative difference in the proportion of time spent in flight exists between typical fliers (Aeshnidae, Cordulegastridae, and Corduliidae) and Libellulidae, most of which would be provisionally classified as perchers; (b) there is a conspicuous lack of data on conspecific density; (c) similarly, there is a near absence of data for Gomphidae; and (d) there is wide variability in the proportion of time spent in flight by libellulids. Note that we include records only if quantitative data were provided or if, for fliers, there was a clear statement or very strong implication that flight was continuous during the period of observation.

Table 2. Behavioural category (flier vs percher), percent time in flight, and behavioural context (e.g. at rendezvous vs foraging) of Anisoptera. F: judged to be a flier; P: judged to be a percher; R: at rendezvous site, FS: at feeding site; EP: from emergent perches; NP: from perches 5 m or more landward from pond edge; L: lower conspecific density, H: higher conspecific density; T: territorial males; NT: non-territorial males.

Family Species	Behavioural category	% time in flight	Behavioural context	Reference
Aeshnidae [1]				
Aeshna cyanea (Müller)	F	100	R	Kaiser 1974
Gomphidae				
Arigomphus villosipes (Selys)	P	2	R	McMillan 2006
Cordulegastridae [1]				
Cordulegaster boltonii (Donovan)	F	86 [2]	R	Kaiser 1982
diadema Selys	F	100 ? [3]	R	Alcock 1985
erronea Hagen	F	100	R	D. Moskowitz pers. comm.
Corduliidae [1]				
Cordulia amurensis Selys	F	100	R	Ubukata 1975
Libellulidae				
Brachymesia furcata (Hagen)	P	18	R	De Marco et al. 2005 [5]
Brechmorhoga pertinax (Hagen)	F	near 100 [4]	R	Alcock 1989
Crocothemis erythraea (Brullé)	P	12	R, EP	Rehfeldt 1991
	P	55	R, NP	Rehfeldt 1991
Diastatops obscura (Fabricius)	P	16	R	De Marco et al. 2005 [5]
Erythrodiplax media Borror	P	9	R	De Marco et al. 2005 [5]
ochracea (Burmeister)	P	5	R	De Marco et al. 2005 [5]
paraguayensis (Förster)	P	<5	R	De Marco et al. 2005 [5]
Erythemis peruviana (Rambur)	P	22	R	De Marco et al. 2005 [5]
plebeja (Burmeister)	P	29	R	De Marco et al. 2005 [5]
simplicicollis (Say)	P	<5	FS	May & Baird 2002
Idiataphe amazonica (Kirby)	P	16	R	De Marco et al. 2005 [5]
Leucorrhinia hudsonica (Selys)	P	3	R	Hilton 1984
Libellula luctuosa Burmeister	P	16	R	Campanella 1975
	P	40	R, L	Moore 1987
	P	43	R, H	Moore 1987
pulchella Drury	P	64	R, L	Pezalla 1979
	P	82	R, H	Pezalla 1979
Micrathyria aequalis (Hagen)	P	19	R	May 1977
atra (Martin)	P	45	R	May 1977
hesperis Ris	P	6	R	De Marco et al. 2005 [5]
ocellata Martin	P	23	R	May 1977
Nannothemis bella (Uhler)	P	<5	R	Hilder & Colgan 1985
Nesciothemis nigeriensis Gambles	P	8	R	Parr & Parr 1974
Notiothemis robertsi Fraser	P	<5	R	Clausnitzer 1998
Orthemis discolor (Burmeister)	P	28	R	De Marco et al. 2005 [5]
Orthetrum coerulescens (Fabricius)	P	13	R	Parr 1983
julia Kirby	P	5	R	Parr 1980
Pachydiplax longipennis (Burmeister)	P	10	R, L	Fried & May 1983
	P	40	R, H	Fried & May 1983
	P	<5	FS	May & Baird 2002
Plathemis lydia (Drury)	P	6	R, L	Campanella & Wolf 1974
	P	49	R, H	Campanella & Wolf 1974
	P	63	R, T	Koenig & Albano 1985
	P	43	R, NT	Koenig & Albano 1985
Sympetrum flaveolum (Linnaeus)	P	8	R	Rehfeldt & Hadrys 1988

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Family Species	Behavioural category	% time in flight	Behavioural context	Reference
Libellulidae (continued)				
Sympetrum sanguineum (Müller)	P	4	R	Rehfeldt & Hadrys 1988
Tholymis citrina Hagen	F	100	R	Miller & Miller 1985a
Tramea binotata (Rambur)	F	61	R	De Marco et al. 2005 [5]
Zygonyx natalensis (Martin)	F	100	R	A. Martens pers. comm.
torridus (Kirby)	F	100	R	Martens 1991
Zyxomma petiolatum Rambur	F	100	R	Miller 1991a

[1] The great majority of species in these families are regarded as fliers, based on casual observation and anecdotal information. Only for the species listed, however, have we found quantitative data and/or unambiguous statements of behavior based on extensive observations over extended periods.
[2] From Kaiser (1982: figs 2, 3); it is not certain that all perched individuals were 'active'.
[3] Described only as "patrolling", no perching noted or implied.
[4] "... patrolled continuously except when sunspots formed adjacent to the stream site (which occurred for brief periods at some, but not all, patrolling locations)." (Alcock 1989)
[5] Data corrected to remove effect of actual mating activity (tandem and copula).

THERMOREGULATORY STRATEGIES

The ability of dragonflies to maintain a relatively constant body temperature (T_b) is determined primarily by climate, body mass and behaviour. All thermoregulatory mechanisms require a source of energy, plus some means of controlling heat gain and loss (May 1978). Heat exchange between a dragonfly's body and the environment can be by conduction, convection, radiation or evaporation. In all kinds of exchange body size is a determining variable because heat exchange is a function of the body surface/volume ratio. Heat production depends entirely on activity of the flight muscles. Dragonflies are typically diurnal, powerful fliers, and they depend on aerial agility during most activities. They are comparatively large, which favours thermoregulation and particularly endothermy (May 1978). During its diel period of activity the adult dragonfly must be ready instantly for very agile flight – to forage, interact with other dragonflies, or escape from predators. In considering the different strategies for thermoregulation available to dragonflies (Table 1), a distinction of fundamental importance is that between ectotherms and endotherms. Ectotherms depend on the ability to modulate external heat sources, especially solar radiation, while endotherms depend on heat produced, by the flight muscles or by wing whirring; the latter activity is normally a prelude to flight, although some species, especially Gomphidae, may prolong wing-whirring to maintain elevated T_b while perched in shade or during cloudy conditions (Miller 1964; May 1976, and pers. obs.). Hence the general behavioural categories of percher and flier are associated principally with the thermoregulatory strategies of ectothermy and endothermy, respectively. Thermoregulation in all dragonflies is facultative and opportunistic, however. All are ectotherms some of the time, but fliers are usually also endotherms that regulate the thoracic temperature by modulating the loss or production of internally generated heat. Conversely, while perchers are normally ectothermic, some may be occasional endotherms by wing-whirring.

Fliers

These are predominantly endotherms, usually large, and typically well insulated by subcuticular air sacs. Because they are continuously on the move, they are less able to control their orientation towards the sun. They can escape from the constraints faced by thermal conformers by controlling the loss or production of heat generated internally by the thoracic muscles. At low ambient temperatures they can raise the thoracic temperature by wing-whirring and reducing cooling rate by restricting haemolymph flow through the dorsal vessel (Heinrich & Casey 1978), thus retaining warm haemolymph in the thorax. At high T_b, typically resulting from sustained flight, they can maximize haemolymph flow, shunting heat to the abdomen, and lose heat rapidly by convection, mainly from the abdomen, which, being long and slender, is well suited for this purpose. Some species increase the effect of abdominal circulation by flexing the abdomen during flight so that its ventral surface is orientated across the wind. By gliding (i.e. reducing wing-beat frequency) they can conserve energy and reduce the rate of heat generation by the flight muscles (May 1995). It is likely, though not proven, that they can offload body heat by evaporative cooling and/or cool themselves by drinking (Corbet 1999: 284, Rüppell et al. 2005). We should note that dragonflies abandon endothermic regulation from time to time, presumably when the energetic cost is too high. They are therefore more appropriately termed "intermittent endotherms."

Perchers

Perchers regulate body temperature predominantly by adjusting body posture in relation to the sun (May 1976, 1977), by microhabitat choice (Clausnitzer 1996; De Marco 1998) and by modifying the time of diel activity (May 1980; De Marco & Resende 2002; Sformo & Doak 2006). Most perchers probably expend less energy than typical fliers do, but may spend long periods foraging (Baird & May 1997). Unlike fliers, perchers apparently cannot control the rate of heat transfer between the thorax and abdomen (Heinrich & Casey 1978; MLM pers. obs.) and thus may have little control of T_b when flying. Perchers are usually thermal conformers or heliotherms. They are much affected by T_a, which determines time of onset of activity and (depending on latitude) the concentration of activity around solar noon. As typical heliotherms, i.e. orientating to the sun to control body temperature, their strategies for increasing T_b include drop-wing perching, basking on insolated surfaces of high albedo (Hilfert 1998) and using wings to reflect radiation onto the abdomen (Tiefenbrunner 1990; Fliedner 2004). To reduce heat gain they can move to shade or, if insolated, adopt the obelisk posture (Corbet 1962) which can reduce the body's shadow by up to 50% (May 1978). Two subcategories of perchers can be recognised, as extremes on a continuum relating to body size.

Small perchers: Their T_b depends closely on T_a, partly because, being small, they have a high surface/volume ratio and are relatively poorly insulated. A large proportion of flights are transition flights, from one microclimate to another, usually necessitated by changes in solar azimuth (Sternberg 1989). They are relatively unlikely to overheat because they are subject to high rates of convective heat loss but may sometimes have difficulty attaining a high T_b. Small perchers can select small

areas of favourable thermal conditions and can control radiant heat loss by making fine postural adjustments. Hence most species remain perched for a relatively long time while at the rendezvous.

Large perchers: Because the capacity to heat the body by irradiation increases with body size (May 1979, 1991; Bartholomew 1981), large perchers can raise the thoracic temperature more efficiently than can small perchers, by basking at lower temperatures. Radiant heat makes up the larger proportion of their heat input. Although exceptions clearly exist, larger perchers are commonly more aggressive towards both conspecifics and heterospecific dragonflies (Pezalla 1979; De Marco et al. 2002; MLM pers. obs).

Apparent anomalies

Fliers

Aeshnids are typical fliers, but at low T_a they sometimes bask in the manner of perchers. In North America, north of the Arctic Circle (66°30'N), in late summer, when the sun appears close to the horizon, aeshnids sometimes rest in conspicuous aggregations on insolated surfaces, for example walls of buildings facing the evening sun. In Gällivare, Sweden, (67°07'N), *Aeshna caerulea* (Ström) adults bask en masse on dark, sealed roads in mid-morning (PSC pers. obs.). At 55°56', in Denmark in early autumn, similar behaviour is exhibited by *Aeshna juncea* (Linnaeus) (Neville 1959), and aeshnids do this even as far south as Calgary, Alberta (51°03'N; G. Pritchard pers. comm.). It is likely, by analogy with *Sympetrum vicinum* (Hagen) (May 1998), that such perching behaviour allows brief feeding sallies when ambient conditions are too cool to make extended flight and/or endothermic warm-up feasible. At high T_a aeshnids exhibit behaviour that arrests endogenous warming. In northeast Spain, at 41°02'N, patrolling male *Anax imperator* Leach (consummate fliers at 50°N) show a slight drop in flight activity around solar noon (Jödicke 1997) and at 36°50'N, in northeast Algeria, in hot weather, adults sometimes remain perched for at least an hour either side of solar noon (PSC pers. obs.). These observations suggest that these individuals had reached the limit of their ability to offload excess heat. So also does the habit of confining patrolling flight to shade, as exhibited by certain species of *Aeshna*, *Somatochlora*, and *Macromia* (Orr 2003; Corbet 2006; Wildermuth 2006).

Crepuscular and eocrepuscular species face special thermal and energetic conditions in that solar heating is not an available option. Such species thus are almost invariably fliers, at least during the twilight phase of their activity. Well known examples that are apparently exclusively or very largely crepuscular include all the Gynacanthini, among Aeshnidae, *Neurocordulia* (Corduliidae), and libellulids such as *Tholymis*, *Parazyxomma*, and *Zyxomma*. Almost certainly the onset of activity in most of these cases is a response to level of illumination rather than to temperature, as clearly described for the gynacanthine, *Heliaeschna ugandica* McLachlan (Corbet 1962). Another noteworthy feature of crepuscular and eocrepuscular activity is that it usually, perhaps always, involves extensive foraging. In at least some instances, e.g. among many gynacanthines, sexual behaviour is rare or absent, and the actual rendezvous site is unknown, although in *Boyeria irene* (Fonscolombe),

e.g., both reproductive and feeding behaviour may be combined (Miller & Miller 1985b). *Heliaeschna* also is known to mate during crepuscular and nocturnal activity (Orr 2003). It is worth recalling that crepuscular feeding swarms are also observed, especially in the tropics and subtropics, in taxa such as *Anax* that are otherwise diurnal. Some crepuscular and eocrepuscular species are very rarely seen at other times and places, but several species of *Gynacantha* and *Triacanthagyna* have been observed at a small, temporary, shaded forest pond in Panama. Most remained apparently inactive, i.e., hanging vertically beneath overhanging palm fronds, but occasional interactions, including apparent mating attempts, as well as oviposition, occurred. None of these activities entailed extended time in flight (MLM pers. obs.). Orr (2003) has noted similar behaviour in *Gynacantha*, *Oligoaeschna*, and *Tetracanthagyna* in Southeast Asia. Whether this represents typical or only occasional reproductive behaviour of these species is uncertain, although Kuribayashi (1965) recorded diurnal flight as a regular feature of activity in *Gynacantha japonica* Bartenev.

Anax junius (Drury), a flier par excellence, can employ both endothermic and ectothermic thermoregulation to raise T_b enough to commence sustained flight. Low light intensity at sunrise stimulates the onset of wing-whirring which allows adults to fly from their roosting sites, which face west and are therefore in shade at sunrise, to east-facing sites where they alight, exposing the body to the sun and, as the sun rises, following the changing thermal gradient until they are basking on the ground (Corbet & Eda 1969; Corbet 1984). Because wing-whirring is energetically very expensive, and because adults may benefit from an early start on days when they migrate (see Wikelski et al. 2006), this strategy may represent an energetically efficient use of the heat sources available, through a judicious combination of endothermy and ectothermy.

The thermoregulatory ability of cordulegastrids has not been investigated, but for most species the rendezvous is at streams that males patrol in continuous flight as do the related chlorogomphids (A.G. Orr pers. comm.). At other times, however, individuals may be found perched in vegetation some distance from streams. They may forage by sallying from these perches, although both *Cordulegaster* and *Anotogaster* sometimes also fly over clearings or roads while foraging.

As mentioned above, gliding is an option available to fliers for reducing heat gain and metabolic energy expenditure in flight. Trameines (sensu Davies & Tobin 1985) are unusual among libellulids in being fliers, although they are more likely to perch than species of *Anax* or *Macromia* (May 1976). Casual observations suggest that the tendency to perch is partly correlated with the occurrence of wind at relatively high T_a; such conditions might increase energy demand, and thus heat production, during flight and also increase convective heat loss by a perched adult (as long as T_b exceeded T_a). One must, at the same time, marvel at the ability of gliders like *Pantala* and *Tramea* to remain in continuous flight for several consecutive hours during the heat of the day near the equator. It can be assumed that they achieve this without overheating partly by gliding, and perhaps also by using small thermals to assist lift, both options being facilitated by possession of a much expanded anal area of the hindwing. The proportion of time spent gliding by *Tramea carolina* (Linnaeus) increases with rising T_a (May 1978). The ability of trameines to remain continuously in flight is prodigious: an individual *T. virginia* (Rambur), at 36°06'N, can spend more than five consecutive hours in continuous flight (Ishida 1958), a feat unlikely

to be possible without extensive gliding. Except for the observations of De Marco et al. (2005), most studies of libellulid gliders pertain to foraging behaviour (see Corbet 1999: 363).

The propensity shown by *Zygonyx* spp. (Libellulidae) for continuous flight and for making liberal use of updrafts near the equator suggests that this may be another group of Libellulidae whose members should be classified as fliers, although it is not obviously adapted for gliding. In the Neotropics, *Brechmorhoga* and *Macrothemis* are two other libellulid genera that seem to behave in a manner resembling *Zygonyx*.

Perchers

Species of *Sympetrum* can be regarded as archetypal small perchers (category 2.1). However, *S. striolatum* (Charpentier) exhibits behaviours which appear to be inconsistent with this placement and which would merit further study. Males sometimes remain on the wing for many consecutive minutes when defending a territory (Ottolenghi 1987). At a site in northern Italy (45°34'N) territorial-defence flight, normally lasting for 2-5 min, could last up to 38 min, the longest such flights occurring when the rate of arrival of females was higher, i.e. at the hottest time of day (Ottolenghi 1987). Noteworthy also is the fact that other small perchers, including *Crocothemis erythraea*, *Trithemis arteriosa* (Burmeister) and *T. kirbyi* Selys, in tropical latitudes, sometimes exhibit protracted territorial flights (M.J. Parr pers. comm.). Trans-oceanic migratory flights of *S. striolatum*, as observed by Longfield (1948) and others, and of other *Sympetrum* also involve a departure from the usual percher behaviour of these species. On very rare occasions, individual *Pachydiplax longipennis* may remain continuously in flight for similar periods during episodes of high conspecific density and intense competition for territories (Fried & May 1983). Species of *Rhyothemis* are generally perchers at the rendezvous but sometimes may soar for long periods, probably feeding, especially over ridges that may deflect air currents upward (Orr 2003).

During much of the day tropical *Micrathyria* are perchers and exhibit typical ectothermic behaviour, but early on cool mornings larger species of the genus remain in continuous flight, apparently so as to maintain a high T_b (May 1977). After T_a exceeds 22°C, they begin to perch, and may allow T_b to drop near to T_a. Other reports of continuous crepuscular or eocrepuscular foraging flights by species that are normally perchers, viz. *Sympetrum sanguineum* (Gorb 1994), *Brachythemis lacustris* (Miller 1982), and *Parazyxomma flavicans* (Martin) (Dijkstra 2003), may be examples of a similar strategy of thermoregulation, as may observations (PSC pers. obs.) of *S. striolatum* swarm-foraging near sunset at about 50°N and of *Stylurus plagiatus* (Selys) doing so before sunrise at 30°N (MLM pers. obs.). Whether cooler conditions require or only permit continous flight in these cases in not certain. In any event, however, these species change their behaviour from percher to flier mode under special circumstances, and in some species, e.g. *Crocothemis servilia* (Drury), *Orthetrum julia* Kirby, heterogeneity may exist within a population such that some individuals behave as 'wanderers' that localise less and fly more than do conspecifics (Higashi 1969; Parr 1980).

Perhaps more serious challenges to the flier/percher dichotomy are several cases of large libellulines, including species of *Libellula*, *Orthemis* and *Plathemis* (but apparently not *Orthetrum*), that rather frequently spend 40-80% of their time in flight (Table 2). Although these fall short of the continuous flight exhibited by typical fliers,

some species that we regard as fliers intersperse periods of perching with flight (e.g. *Tramea*, Table 2); so it would be inconsistent to nominate uninterrupted flight as a criterion for categorising the species under discussion here as fliers. We are inclined to classify these large libellulines as perchers. In some instances, very high flight frequency and/or duration is/are associated with territorial defence at high density (e.g. *Plathemis lydia*, Table 2). These species are mostly very robust and highly aggressive, even attacking heterospecifics readily. This of course means that they may be under frequent and intense stimulation from rivals. On the other hand their bulky thoraxes and rapid flight probably subject them to the risk of overheating, since the large percher, *Libellula saturata* Uhler, is unable to shunt haemolymph to the abdomen to accelerate convective cooling (Heinrich & Casey 1978). This inability argues against their being able to fly for long periods at high temperature, and indeed *L. saturata* reduced its activity at midday. We predict that these and related species will be found to behave as 'standard' perchers when T_a is moderate (i.e. not too high) and when the density of potential rivals (including heterospecific individuals) is low. Nevertheless, thermoregulatory behaviour and physiology, and foraging and flight behaviour across a wide range of intra- and interspecific male density, require further detailed study.

Finally, one species, *B. lacustris*, studied by Miller (1982, 1991b) in Kenya and Zimbabwe, appears to span the divide between perchers and fliers, as the nature of their activity changes. They feed in flight near dawn and at evening twilight, roost in close proximity (in a nearly horizontal posture along the sides of plant stems) with occasional feeding sallies during much of the day, and at around 15:30 h males begin to perch at the waterside, holding territories from which they fly out and court females. Thus they evidently are fliers when feeding and males, at least, perch at the rendezvous. Some overlap occurs at the onset of crepuscular feeding, as territorial males may continue for a time to perch between pursuits of flying females.

DICHOTOMY OR CONTINUUM?

This inventory of the attributes of fliers and perchers reveals a dichotomy based on behavioural mode, morphology, methods of thermoregulation and presumably of metabolic energy expenditure. This classification has descriptive, and, to a large extent predictive, value. By observing a dragonfly's behaviour, especially with regard to the time it spends in flight, one can generally infer its status as a thermoregulator and, if duration of activity can be determined, an estimate of its energy requirements. We suggest that most departures from expectation can be attributed to 'forces majeures' deriving from interspecific or intraspecific competition at the rendezvous. We consider that a distinct dichotomy, albeit with some behavioural overlap, exists between fliers and perchers and that a continuum, perhaps reflecting differences in size, abundance, and mating strategy, exists within each major category (De Marco et al. 2005). If the dichotomy hypothesis is to be rendered more secure, i.e. given greater predictive value, we see several directions in which future research will be needed.

(1) Explicit and, if possible, quantitative evaluation of responsiveness of species across a broad behavioural and taxonomic spectrum to potential prey (or prey models) and other dragonflies. This should allow a much clearer distinction between individuals that are 'active' vs those 'at rest'.

(2) Expanding Table 2 by classifying additional species as fliers or perchers according to their behaviour and then determining their method of thermoregulation and innate temperature thresholds for flight, as done, e.g., by Heinrich & Casey (1978) and May (1976). The resulting data would be much more informative if accompanied by objective measures of the proportion of time spent in flight and the level of inter- or intraspecific interaction among adults at the site. Such data would not only clarify more fully the meaning and distinctness of the flier and percher categories but would offer the possibility to infer energy budgets for the species and behavioural circumstances observed. Of particular interest are the relatively small number of libellulids that have apparently become fliers; corduliids such as *Williamsonia* and *Cordulephya* that are perchers; the few aeshnids that regularly employ both tactics depending on environmental conditions; and nearly all gomphids, especially those that may, at times, fly for relatively long durations.

(3) Identifying species that, by the same criteria, would be classified as fliers or perchers but whose behaviour, either usually or occasionally, seems to be inconsistent with this, and then seeking to rationalise any apparent anomalies in terms of what is known about the species' behaviour, ecology and thermal environment. We have identified above a few such apparently anomalous situations which we suggest might repay close scrutiny.

(4) In particular, determining whether species normally observed to be crepuscular and/or eocrepuscular fliers are engaged in both foraging and reproductive behaviour or only in the former. Such cases might provide very informative tests both of our suggested framework for defining activity and of the possible limitations of the distinction between fliers and perchers.

(5) Investigating in detail the behaviour of more tropical species, especially fliers and species that are predominantly forest dwellers. Information on diel periodicity of activity and on possible changes in behaviour with altitude may be of particular interest.

(6) Including many more observations of time allocation to perching and flight during foraging behaviour. D.R. Paulson (pers. comm.), based on extensive but largely qualitative observations, has argued that the percher-flier dichotomy may be more clearly apparent in these circumstances than at the rendezvous and that, indeed, the evolution of alternative modes of activity may be strongly influenced by foraging behaviour. Thermoregulatory patterns then would follow secondarily from perching or flying behaviour.

We conclude that there is merit in retaining the bipartite classification of dragonflies into fliers and perchers, together with the thermoregulatory capabilities assigned to them, as defined and refined in this article. Specifically, we conclude that (subject to a small number of unexplained anomalies) the distinction between fliers and perchers among Odonata constitutes a dichotomy sufficiently incisive to be a useful predictor of the suite of thermoregulatory strategies and of many aspects of time and energy budgets that representatives of each category employ. Intra- and interspecific density at the rendezvous may, on occasion, distort the normal (species-specific) proportion of time spent in continuous flight; but this phenomenon can be readily observed and taken into account. The causal link between species in either category and their means of thermoregulation has to be qualified to the extent that there is a

continuum within each category with respect to body size and the consequent degree of reliance on endothermy. The status of a species within this classification cannot be inferred purely on taxonomic grounds, and it is clear that both percher and flier behaviour have evolved independently several times (J. Ware pers. comm.). Nevertheless, with very few exceptions, Zygoptera and smaller Libellulidae are perchers, and Aeshnidae and Corduliidae are fliers. At the same time the flier/percher dichotomy is likely to be useful heuristically if it points up anomalies with respect to expectation based on taxonomic affinity, e.g. libellulids that, like *Tramea*, appear especially adapted for gliding, as well as *Zygonyx* and *Brechmorhoga* and their relatives, because this will encourage close examination of species that face anomalous circumstances or that make special arrangements to thermoregulate in atypical ways. We have entitled this essay "a provisional reappraisal", recognising that at present quantitative records of the proportion of time spent in flight by adults of both categories, together with concurrent measurements of ambient temperature, are unacceptably few and that we welcome the prospect of a survey being conducted to elicit more such records from practising odonatologists and thus to place the flier/percher hypothesis on a firmer footing.

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