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DRAGONFLIES AND THE THERMAL LANDSCAPE: IMPLICATIONS FOR THEIR CONSERVATION (ANISOPTERA)

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The National Botanic Gardens, Pietermaritzburg, South Africa are being partially ecologically landscaped. Odon. are one of the subject groups for conservation. Their behaviour relative to the topography and thermal patterns of the landscape were studied. Several spp. of Anisoptera used the vegetation, rocks, gravel and sand substrates for perching. There were distinct species- and sex-specific behavioural responses to the shape and features of the landscape. By selecting certain microhabitats, and substrates, the dragonflies gained extra warmth late in the afternoon, particularly late in the season. Rock-basking was particularly prominent, as was aggregating in a sheltered hollow. These behavioural patterns apparently allowed longer periods of activity, especially for hunting crepuscular prey and searching for suitable roosting sites. Rocks and the hollow were not used at night when cold-air drainage made the habitat too cold. These behaviours are important in the lives of the dragonflies, to the extent that local topography and landscape features should be considered when managing areas for dragonfly conservation.

INTRODUCTION

The three-dimensionality of landscape has a major influence on insect meso- and micro-distribution, and it is important to consider the vertical aspect of the landscape when selecting areas for the creation of reserves (SAMWAYS, 1989, 1990). Dragonflies are under world-wide threat from habitat destruction and pollution (MOORE, 1982). Natal has a rich dragonfly fauna, including 72% of the species from the South African region (PINHEY, 1984). It also has rapid rates of urban expansion and destruction of natural habitats. In such situations, reserves, even botanic gardens, can be important refugia. Elsewhere it has been shown that management of habitats within reserves has succeeded in increasing

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population sizes and dragonfly diversity (MOORE, 1976).

Adult Anisoptera are mostly strong and powerful fliers, and most activities such as foraging, territory patrolling, mating and oviposition, are performed on the wing. The home-range of an individual or population in its lifetime is thus considerably larger than for most other insects. Their strongly directional flight permits anisopterans to actively select appropriate microhabitats from a landscape on a much larger scale than smaller, less mobile insects.

Anisopterans have been shown to maintain a body temperature relatively independent of ambient air temperature (Ta) (MAY, 1978). Such thermoregulation in Anisoptera is either endogenous, by increasing metabolic heat production, or exogenous, by heliothermy, postural adjustment and the selection of thermally suitable microhabitats (MAY, 1976). These behavioural attributes permit them to exploit spatially variant microclimates across landscapes, and optimize activity patterns by short-term regulation of body temperature (Tb) (MAY, 1976; TRACY et al., 1979; DAVENPORT, 1985). Many species regularly select thermally different microhabitats and show species-specific behavioural thermoregulatory mechanisms (SHELLY, 1982).

This paper investigates how several dragonflies respond to the local thermal landscape in a partly ecologically landscaped botanic garden in South Africa. The results are then used in making suggestions for maintaining dragonfly diversity. There are also wider implications for dragonfly reserves in general (SUGIMURA, 1989; MOORE, 1982, 1987).

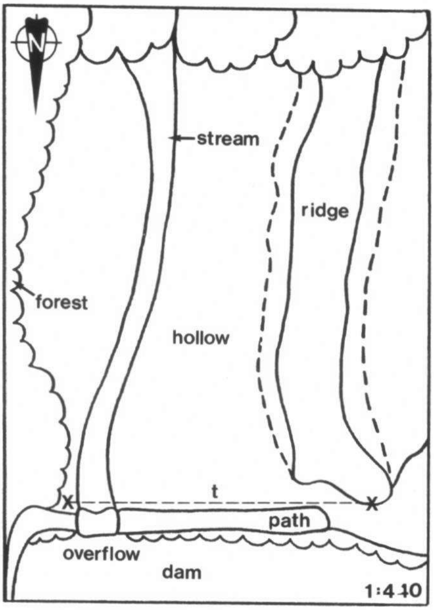


Fig. 1. Plan of the study area indicating landscape elements and division of zones. — [Profile-transect (t) seen in Fig. 2]

SITE AND METHODS

Site

The site was a 40 m x 45 m area in the National Botanic Gardens, Pietermaritzburg, Natal, South Africa (30°20′, 29°36′, 690 m a.s.l.) (Fig. 1). The southern boundary of the site was a sand path leading to a man-made dam wall with overflow. This dropped about 3 m down into a narrow stream, in a natural depression (Figs 2, 3). The eastern perimeter was the vegetation-covered bank of the stream, rising into the verge of a coastal tropical forest area (ACOCKS, 1988). The western perimeter was another steep vegetation-covered

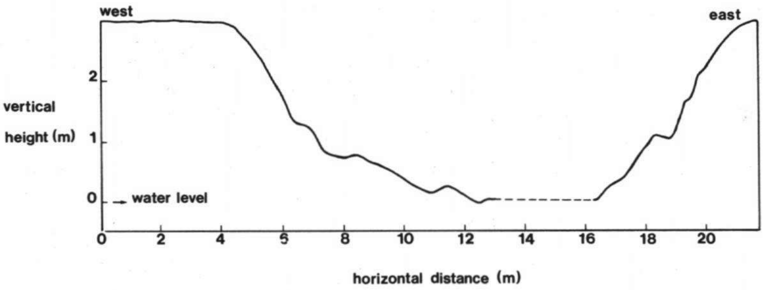


Fig. 2. Hollow-profile taken along the border of the dam-wall, path, and hollow on an east-west transect.

bank rising from the hollow onto a regularly mown grass-covered ridge, about 3 m wide. A short path led into the hollow from the south-western corner. The vegetation in the hollow consisted of mixed disturbed grassland and areas of open gravel substrate. Within the hollow, were a number of stones and rocks (± 0.5 m^3), and a dumped flat concrete slab, 1 m x 0.5 m. Observations on the dragonflies were centred principally around the rocks.

Fig. 3. The hollow as seen from the western end of the dam-wall.

Methods

Data were collected on 36 days between 9 January 1990 and 31 May 1990, at various times of the day between 06h00 and 19h00. Anisoptera were identified using binoculars, and a permanent voucher collection was made.

Ambient air temperature (Ta), rock-substrate temperature (Tr), water temperature (Tw) and relative humidity (% rh) were taken with a Thies Clima digital hygrothermometer. Ta readings were taken at hourly intervals, shading the instrument, in the centre of the hollow and above the hollow on the dam wall path. Humidity readings were taken concurrently and later converted to vapour pressure (kPa) for purposes of comparison (SAVAGE, 1988). Dam and stream temperature (Tw) were measured once every visit. Rock-surface temperatures (Tr) were read one minute after allowing the shaded patulate probe to acclimatize against the rock surface. Cloud-cover (% cc) was categorized as 0-20%, 20-50%, 50-80%, 80-100%.

Behavioural observations. — Every hour, the number of mature perched or flying dragonflies within each zone was censused without disturbing them. Positions of perching and posture were noted for all individuals of all species. Dragonflies in the study area were predominantly males, although females were included in the census (Tab. I). Only *Orthetrum caffrum, O. julia falsum* and *Crocothemis erythraea* females were recorded regularly. The behaviour, posture, time and duration of rock-basking by species was closely observed. Rock-basking refers to the behaviour where dragonflies absorbed heat from the rock surface while posturing on it. Certain individuals and species consistently used rocks in the hollow for basking. Two additional, experimental rocks (± 0.5 m^3) were placed 1.5 m from the other two rocks and 1.5 m apart.

Experimentation. — To determine whether it was rock temperature that attracted individuals, the rock in the hollow that was most consistently used by rock-basking species was packed with ice-bags and covered with DPX foam-matting between 8h00 and 14h30 on three alternate, warm, clear days. Before removing the ice-packs and DPX-matting, temperatures of the other rocks wre determined. A rock, adjacent to the experimental one, was left exposed as the control, and all remaining rocks were covered over with cut grass. The behaviour of basking individuals was then observed. The experiment was repeated on days 1, 3 and 5 to prevent the possibility of basking individuals learning to avoid the experimental rock.

SPECIES SEASONALITY

Fourteen species were recorded (Tab. I). Figure 4 shows the regularity of occurrence of each species in the area. *Trithemis arteriosa* (1-60 individuals), was consistently the most abundant species throughout the five months. *T. dorsalis* and *T. furva* were treated together as both were present in the area, yet the males of the two species are indistinguishable in the field. These two species, as well as *T. stictica,* were present in moderate numbers (1-15 individuals). Between 1 and 10 *Orthetrum caffrum* and *O. julia falsum* individuals were regularly present. *Zygonyx natalensis* (1-4 individuals) were present on all occasions until the end of

Table I

Anisopteran species recorded at the study site and list of abreviations used in the figures

Species	Abbreviation
Anax imperator mauricianus Ramb.	A.i.
A. speratus Hag.	A.s.
Ceratogomphus pictus Hag.	C.p.
Crocothemis erythraea (Brullé)	C.e.
C. sanguinolenta (Burm.)	C.s.
Nesciothemis farinosa (Först.)	N.f.
Orthetrum caffrum (Burm.)	O.c.
O. julia falsum Longfield	O.j.f.
Pantala flavescens (Fabr.)	P.f.
Trithemis arteriosa (Burm.)	T.a.
T. dorsalis (Ramb.)	T.d/f.
T. furva Karsch	T.d/f.
T. stictica (Burm.)	T.s.
Zygonyx natalensis (Martin)	Z.n.

March. Three to four individuals of *Nesciothemis farinosa* and *Ceratogomphus pictus* appeared intermittently until mid-April and mid-May respectively. *Crocothemis erythraea* became especially abundant (up to 30 individuals) between mid-March and mid May. *C. sanguinolenta* (1-4 individuals) were sighted only between 6 April and 3 May. *Anax imperator* and *A. speratus* only occasionally flew over the study area, and *Pantala flavescens* was noted once perching on the ridge and then in the hollow. After 19 May the only Anisoptera remaining were *O. caffrum* (1-2 individuals) and *T. arteriosa* (1-5 individuals).

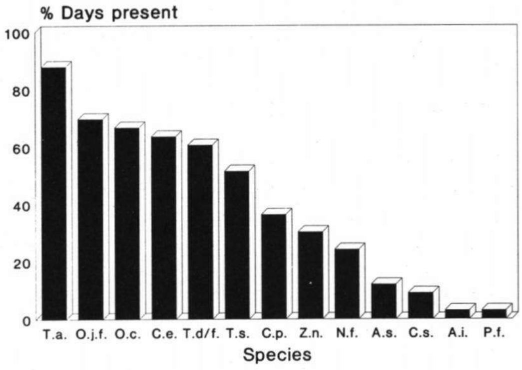


Fig. 4. The regularity of occurrence of anisopteran species in the study area. — [Species abbreviations as in Tab. I]

WEATHER PERIODS CORRESPONDING TO CALENDAR DATES

The five-month period was divided into five "weather periods", rather than simply using the boundaries of calendar months, as this was a more realistic division from the viewpoint of the dragonflies. The five periods corresponded to the calendar dates 9 to 29 January, 30 January to 2 March, 3 March to 11 April, 12 April to 5 May and 6 May to 31 May (Tab. II). These weather changes were based on changes in dam and stream water temperatures in combination with fixed time, % cc and Ta readings. Water temperature appeared to be a better overal indicator of seasonal change, as it did not fluctuate as greatly with daily weather variations as did Ta (Tab. II).

Table II
Mean climatic readings (± 1 S.E.) for the five weather periods (14h00-18h00)

Weather period	*1* (N=8)	*2* (N=5)	*3* (N=11)	*4* (N=5)	*5* (N=7)
Date	9 Jan - 29 Jan	30 Jan - 2 Mar	3 Mar - 11 Apr	12 Apr - 5 May	6 May - 31 May
Air Temp. (°C)	30.68± 2.05	27.80± 1.22	25.70± 0.79	24.70± 1.25	24.90± 1.02
e (kPa)	108.70±50.73	78.64±18.29	285.21±95.61	205.40±82.73	65.76±23.60
Dam Temp. (°C)	25.80± 0.79	26.00± 1.06	22.40± 0.43	21.60± 1.20	19.60± 0.29
Stream temp. (°C)	23.40± 0.79	21.80± 0.75	19.90± 0.42	19.30± 1.16	16.60± 0.29

DRAGONFLY UTILIZATION OF THE LANDSCAPE

DAILY DISTRIBUTIONAL CHANGES

The tall vegetation on the ridge was the first zone to receive direct sunlight, and on sunny mornings, activity was centred here first. Activity occurred over the water from morning to mid-afternoon under sunny conditions. From mid to late afternoon, and early evening, certain species shifted from surrounding zones and from other areas of the Gardens into the hollow (Fig. 5). There were no distinct differences in numbers of individuals between zones except for this marked increase in mean number of dragonflies in the hollow between 14h00 and 17h00. Individuals of nine species occurred in the hollow between 14h00 and 18h00 (Fig. 6). Other patterns of daily movement between zones were obscured by daily weather fluctuations such as cloud cover and rain. A likely explanation for the peak at 13h00 in Figure 5 is that all the readings constituting this mean were taken on days with over 50% cloud cover. Despite these obscuring factors, however, the hollow is highly important as an activity spot or congregation point.

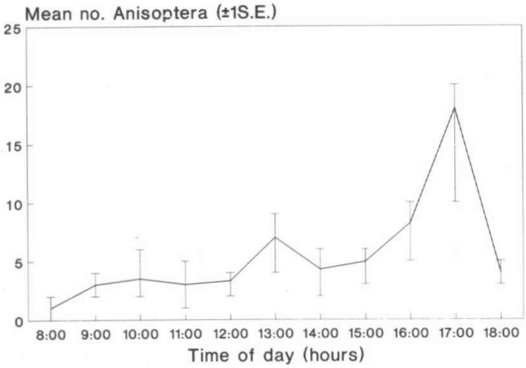


Fig. 5. Daily, late-afternoon shift of anisopterans to the hollow.

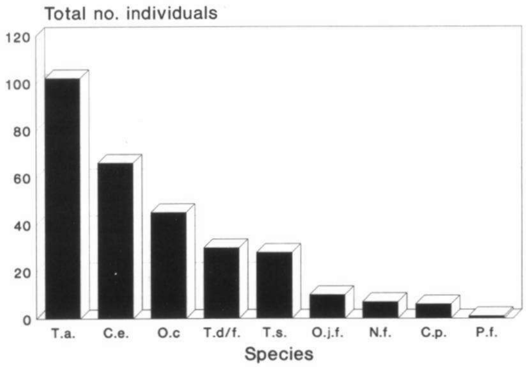


Fig. 6. Abundance of anisopteran species in the hollow between 14h00 and 18h00. — [Species abbreviations as in Tab. I]

SEASONAL DISTRIBUTIONAL CHANGES

Additionally, within the same daily peaking time period, 14h00 to 17h00, there was an increase in the abundance of Anisoptera in the hollow from midsummer to early winter (Figs 7a, 7b). These dragonflies were mostly late-reproductive and post-reproductive individuals, as evident by tattered wings and/or browning (PINHEY, 1951). The drop in abundance in all zones in weather period 5 (Figs 7a, 7b) was the result of populations dying off in late season. Although the trend in changing abundance of individuals in the remaining zones was not as evident as it was in the hollow, there was a steady decrease in individuals over the water with season (Fig. 7a).

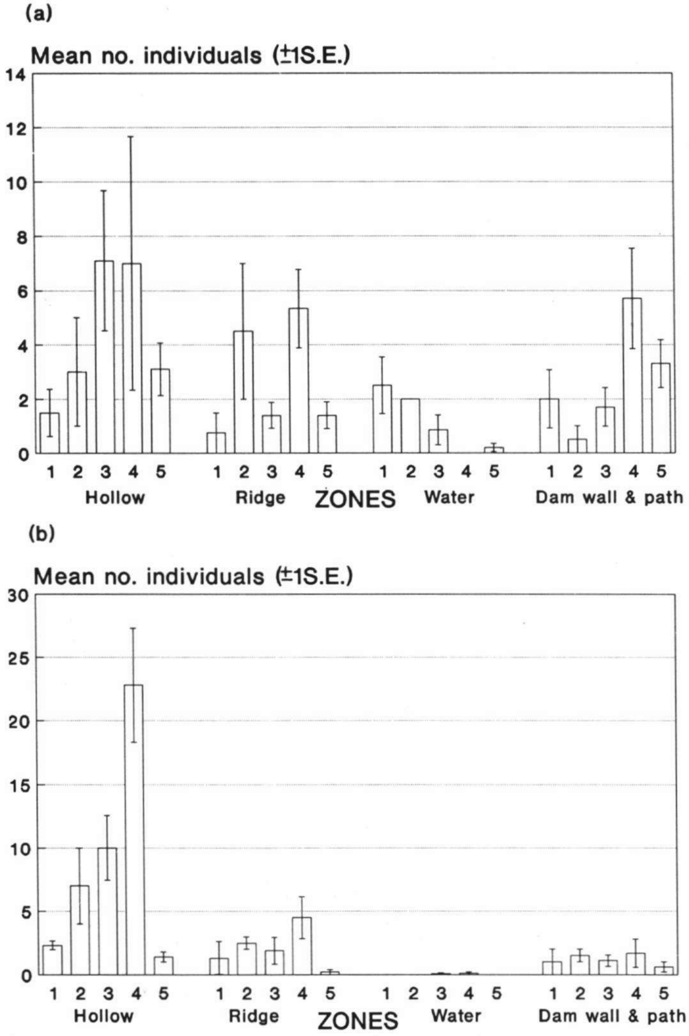


Fig. 7. Number of Anisoptera in zones over the study period, between (a) 14h00 and 16h00 and (b) 16h00 and 18h00. — [Weather periods, 1-5, as in Tab. II]

The peak for period 4 on the dam-wall and path (Fig. 5a) is attributed to species which used the sandy surface of the path as a secondary heat source during the late afternoon. This was often in the absence of direct sunlight (irradiance) when the Ta of this weather period was low (Tab. II).

Between 16h00 and 18h00 (Fig.7b) there was a distinct absence of individuals over the water, and a marked reduction in numbers on the ridge and dam-wall and path. The ridge was the last of the zones to receive direct sunlight before sunset, which may explain the peak, with dropping mean Ta (Tab. II), at weather period 4 (Fig. 7b). The number of individuals present in the hollow at this time remained high particularly during weather periods 3 and 4.

DIVISION OF ACTIVITIES BETWEEN ZONES

Between 14h00 and 18h00, individuals in the hollow perched on the vegetation, and from here made occasional foraging trips. Others used open patches of ground and rocks for basking. Overnight roosting in the hollow was rare, only three individuals of *C. erythraea* being recorded here.

As the hollow received direct sunlight 0.5-1.0 h later than surrounding zones, the ridge vegetation was favoured by individuals basking in early morning, as well as in the late afternoon sunshine. Foraging along the ridge at various times of the day was dependent on the presence of abundant prey, e.g. midge swarms. *C. erythraea* was the most common forager on the ridge.

Rocks on the dam wall were used as substrates for sun-basking and as foraging perches. The dam-wall path was sometimes used during mid to late afternoon for ground-basking, extensively by *T. arteriosa* and occasionally by *T. dorsalis/furva* and *N. farinosa.*

Between mid-morning and early afternoon the overflow, waterfall and stream were used for territorial behaviour, oviposition and foraging mostly by *T. arteriosa, T. dorsalis/furva, Z. natalensis, O. julia falsum,* and *C. pictus.*

MICROCLIMATIC CONDITIONS

There was no significant difference between temperature or vapour pressure in the hollow compared with those above the hollow (Tab. III).

There was a highly significant increase in mean number of dragonflies in the hollow under conditions of 0-20% cc versus 20-100% cc (Kruskal Wallis test, $K=12.4$, $d.f.=1$, $P < 0.01$) (Tab. IV). On overcast days, overall abundance was also very low with none to one or two in the hollow, and some perching on the ridge or dam-wall path vegetation.

Table III
Mean temperature and vapour pressures between 16h00 and 18h00 (± 1 S.E.)

Weather period	°C kPa	In hollow	Above hollow	N
9 Jan - 29 Jan	Temp	30.4 ± 1.8	29.7 ± 2.9	2
	e	94.2 ± 36.3	88.5 ± 16.8	
30 Jan - 2 Mar	Temp	28.1 ± 2.9	28.3 ± 2.7	2
	e	339.9 ± 234.6	376.3 ± 249.0	
3 Mar - 11 Apr	Temp	24.6 ± 0.9	23.7 ± 1.1	8
	e	346.5 ± 49.8	307.3 ± 75.4	
12 Apr - 5 May	Temp	23.6 ± 0.7	23.1 ± 1.1	8
	e	336.9 ± 91.8	307.3 ± 75.4	
6 May - 31 May	Temp	19.2 ± 0.6	18.7 ± 0.6	6
	e	310.7 ± 40.8	288.2 ± 60.3	

Table IV
Mean and range of number of Anisoptera in hollow with varying percentage cloud cover ($P < 0.01$)

% c.c.	Mean no. Anisoptera (± range)	N
0- 20	5.8 ± 1.29	32
20- 50	12.4 ± 5.70	5
50- 80	9.4 ± 1.52	8
80-100	20.4 ± 4.65	9

UTILIZATION OF MICRO-HABITAT FEATURES

T. arteriosa, O. caffrum, C. erythraea, N. farinosa, C. sanguinolenta and *O. julia falsum*, regularly basked on the rocks or on the ground of the hollow, and on the dam-wall path. These species showed typical thermoregulatory behaviour in microhabitat selection and postural adjustment.

ROCK-BASKING BEHAVIOUR

Rock-surface temperatures on clear, sunny days exceeded ambient air temperature from mid-morning until early evening (Tab. V). Figure 8 shows the five species that basked on rocks. Individuals flew directly from outside the hollow or from grass perches in the hollow and landed on the rocks. They immediately adopted a horizontal position, with the wings held down partly in contact with the rock surface. The thorax was either slightly raised or sometimes in direct

Table V
Mean difference (± 1 S.E.) between ambient and rock-surface temperature over weather periods

Weather period	Rock - air temp °C	N
9 Jan - 29 Jan	7.1 ± 1.09	7
30 Jan - 2 Mar	10.6 ± 1.56	5
3 Mar - 11 Apr	5.1 ± 0.84	11
12 Apr - 5 May	6.2 ± 0.79	9
6 May - 31 May	6.5 ± 0.80	9

contact with the surface. The abdomen was generally held off the rock surface, horizontally to it. On occasions the entire ventral surface of the dragonfly, wings, thorax and abdomen, were in contact with the rock. During rock-basking, there was the occasional raising or lowering of the thorax. Head movements and grooming of compound eyes and antennae with the forelegs sometimes also occurred. Long periods of basking were interrupted by short flights off the rock to return to a new position. These appeared to be re-positioning and not foraging flights, as they seldom extended further than 0.5 m away from the rock and were circular. Individuals remained on a single rock between five minutes to over an hour. Sometimes, they changed rocks during daily rock-basking. If disturbed during rock-temperature measurement, the dragonfly always either returned to the rock, or re-positioned itself on a nearby one.

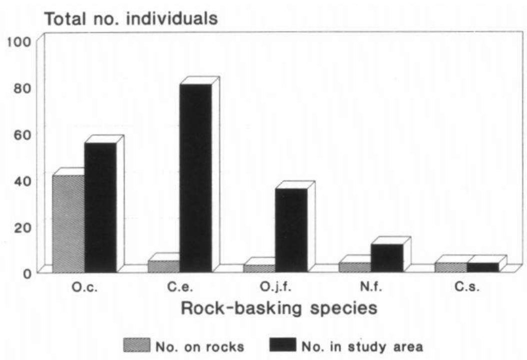
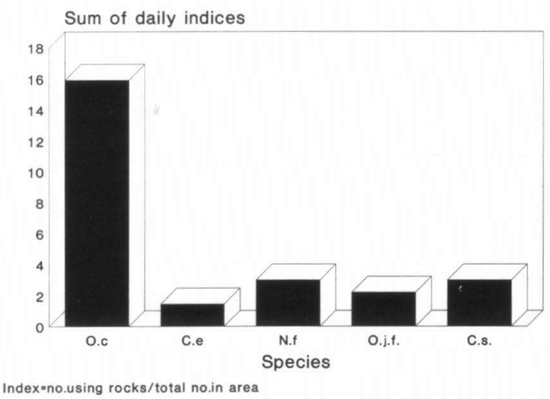


Fig. 8. Extent of rock-usage by rock-basking species in the hollow. Total over study period. —[Species abbreviations as in Tab. I]



Index=no.using rocks/total no.in area

Fig. 9. The relative importance of rocks to rock-basking species in the study area. — [Species abbreviations as in Tab. I]

The rocks on the dam-wall were never used as basking substrates, but rather as perches for foraging or territory patrolling. These rocks had temperatures consistently 2-3°C lower than those in the hollow as they were in the water of the dam-wall overflow. Dragonflies were often seen in the obelisk position on the dam wall rocks, but never in this position on the rocks in the hollow.

O. caffrum was the most consistent in its rock-basking behaviour in the hollow. Figure 9 gives the relative usage of the rocks by all the rock-baskers in the hollow, based on an index of proportion of individuals of a species, in the study area, basking on the rocks.

Towards the end of April, the vegetation around two of the rocks became overgrown. These rocks were no longer used for basking, in preference for other rocks in the open. After removing the vegetation around the rocks, one day at a time, *O. caffrum* males basked on them the following day.

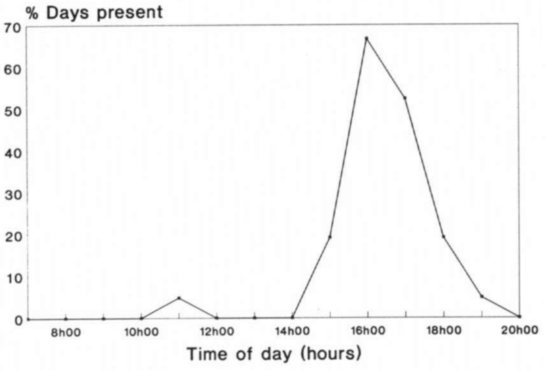


Fig. 10. Time of day and occurrence of rock-basking in the study area.

DAILY AND SEASONAL ROCK-BASKING

Rock-basking behaviour occurred almost entirely between 14h00 and 18h00 each day, varying only slightly with daily weather conditions (Fig. 10). Basking extended long after rocks were no longer sunlit. Individuals often only arrived after the rocks were shaded. This behaviour increased substantially between weather periods 1 and 5 (January to May) for *O. caffrum,* and less so for *C. erythraea* and *O. julia falsum* (Fig. 11). *O. caffrum* was the only species which used the rocks throughout the five weather periods. *C. erythraea* and *O. julia falsum* only occasionally basked on the rocks. Rock-basking in *N. farinosa* was highest in weather period 1, dropping in 2. Individuals of this species were still present in the study area into the beginning of the fourth weather period, but no further basking was observed. The two to three *C. sanguinolenta* individuals were seen rock-basking for the entire time they were present in the study area.

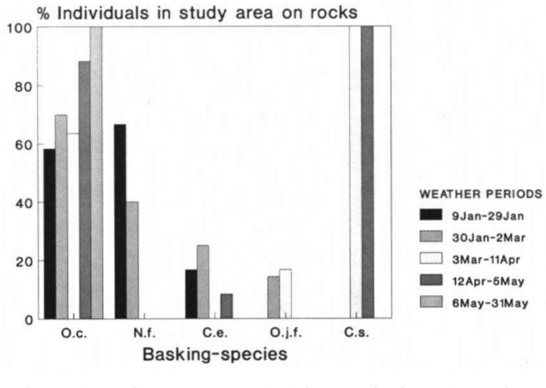


Fig. 11. Use of rocks by rock-basking species in each weather period. — [Species abbreviations as in Tab. I]

EXPERIMENTAL MANIPULATION OF ROCK TEMPERATURE

On day 1 at 13h40 an *O. caffrum* male flew into the hollow and landed on the experimental rock. The surface-temperature of this rock was lower than the other rocks (Tab. VI). The male took off again after only three seconds and hovered above the rock, alighted again for two seconds and then flew off to bask on the control rock, where it remained for 29 minutes. Day 3 and 5 produced similar results. On both occasions an *O. caffrum* male arrived, alighted briefly on the experimental rock, hovered above it and then flew off to the control rock.

PREFERRED TEMPERATURE RANGE FOR ROCK BASKING

Figure 12 shows the temperature range at which Anisoptera basked on the rocks.

Table VI
Rock temperatures (experimental rock versus others in hollow) after experimental manipulation (14h30)

Day	Ta (°C)	Mean rock temp. ± 1 S.E. (°C)	Exp. rock temp. (°C)
1	24.2	29.2 ± 0.73	19.2
3	20.7	25.2 ± 0.59	19.0
5	24.8	31.6 ± 1.2	19.6

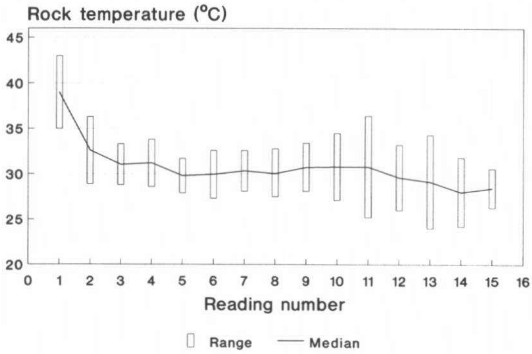


Fig. 12. Range of rock temperatures (upper temperature at which individual alighted and lower temperature at which it flew off) at which Anisoptera basked on rocks between 30 January and 17 May.

WING-WHIRRING

Wing-whirring was seen only twice, both by male *O. caffrum* individuals. On the first occasion (6 May) the male settled on the rock at 15h20 at a Tr of 34.3°C. It remained on the rock, repositioning itself only twice, until 16h35. It then raised and shook its abdomen, lifted the thorax, and rapidly raised and lowered its wings for about 30 seconds. It then flew off and out of the hollow. Ta at 14h40 was 19.2°C and Tr was 24.0°C. The same day another *O. caffrum* male on a rock in the hollow flew off at 16h50, at a Tr of 24.2°C, without any sign of wing-whirring. On 17 May a male landed on a rock (30.6°C) at 15h15. At 16h09 it flew off after wing-whirring for 45 seconds. Ta was 17.2°C and the rock surface 26.3°C. Both times that wing-whirring occurred, the temperature in the hollow was below the average (19.18±0.63°C (±1 S.E.)), at which any anisopteran activity was observed in the study area. It was also below the mean Ta for the hollow at that time during weather period 5 (Tab. III).

GROUND BASKING

Basking on the ground involved the same posture as on the rocks. *T. arteriosa* males and *O. caffrum* females regularly exhibited ground-basking. *T. dorsalis/furva, N. farinosa, C. pictus* and *C. sanguinolenta* ground-basked less frequently. *T. arteriosa* and *T. dorsalis/furva* were only seen basking on the sandy dam-wall path. *N. farinosa* basked both on the dam-wall path and on the gravel patches in the hollow. The other species basked only on the gravel in the hollow.

O. caffrum females used both rocks and ground for basking, whereas males were regularly seen on rocks, but never on the ground. A Chi-squared test with Yates' correction on the proportion of the sexes using rocks and ground was highly significant ($\chi^2 = 9.73$, d.f. $= 1$, $P < 0.01$).

EFFECT OF CLOUD COVER

A Kruskall-Wallis test showed no significant difference ($P > 0.05$) between % cc and the number of rock-basking individuals.

INTRA- AND INTERSPECIFIC INTERACTIONS

Very little interaction occurred either intra- or interspecifically among individuals, on vegetation, rocks or ground, in the hollow. There were no signs of aggression between any individuals. *C. erythraea* and *T. arteriosa* perched on vegetation in fairly tight aggregations, often with many males close together. Often two to three individuals basked on the same rock e.g. two *O. caffrum* males and one female, or two *O. caffrum* males and one male *N. farinosa.*

DISCUSSION

BODY-TEMPERATURE REGULATION

CORBET (1983) divided Anisoptera into fliers and perchers on behaviour and body-temperature (b) regulation. Fliers regulate Tb endothermically, whereas perchers regulate Tb predominantly ectothermically. Fliers do not react as strongly as perchers to daily temperature fluctuations, although alteration of flight pattern between wing-beating flight and gliding occurs as a temperature response (CORBET, 1983; MAY, 1976). Only four species here were fliers: *A. imperator, A. speratus, P. flavescens* and *Z. natalensis.* The remaining ten species were perchers and showed some form of ectothermy.

AGGREGATION IN THE HOLLOW

During late afternoon to early evening, increasingly so with the approach of winter, the dragonflies distinctly grouped in the hollow.

The temperature/vapour pressure in the hollow was not significantly different from surrounding zones, when measured 1 m above the ground. Behaviourally more important differences did occur closer to the ground, in what GEIGER (1971) terms "temperature stratification near the ground". The hollow was sheltered from wind on all sides and in such sheltered areas, on clear days, evaporative cooling is reduced and air and soil temperature is substantially higher than in non-sheltered areas (GEIGER, 1971). The temperature difference can be 7°C higher 5 cm above the ground, and decreases with increasing height. The mean height of individuals perching on vegetation in the hollow between 14h00 and 18h00 was 0.79 ± 0.047 m (± 1 S.E., n=14).

The patches of grass and other vegetation in the hollow provided perching dragonflies with further shelter. Humidity is higher and evaporative cooling is reduced in vegetation near the ground. Dragonflies perched here are under reduced thermal stress (CLENCH, 1966; GEIGER, 1971; MAY, 1978). In comparison with the hollow, the dam-wall and path were very exposed to wind.

Abundance of individuals in the hollow peaked at 17h00. This phenomenon of aggregation fits GAMBLES' (1971) definition of a dragonfly dormitory i.e. "regular aggregations of individuals in one spot". Although some dragonflies do spend resting periods in aggregation (GAMBLES, 1971), the hollow was not a regular roosting site for any of the species, all leaving the area shortly after 18h00.

Temperature and irradiance are the important factors in the choice of nocturnal roosting sites by dragonflies. Onset of roosting, as well as the start of activity in the morning, is determined by a combination of these factors. Nocturnal temperature inversions are a strong influence on local climate in the Natal uplands (TYSON, 1968). The hollow, receiving less irradiance than surrounding high points and also subject to nocturnal temperature inversions (YOSHINO, 1975), is a preferred late-afternoon aggregation site but not a preferred night-time roosting site. MAY (1977) suggested that *Micrathyria ocellata* warms up on a perch and then flies off just in time before being "trapped" by temperatures falling below minimum flight/Tth threshold. This appeared to be the case, particularly with *C. erythraea*, in the hollow.

"Vesper warming", a behaviour described in butterflies, is warming behaviour by individuals in the late afternoon before finding cover for the night, and it maintains Tb at operational flight level for as long as possible (CLENCH, 1966). Aggregation in the hollow, rock- and ground-basking in this dragonfly assemblage closely parallels that of vesper warming in butterflies. Butterflies share a number of similar behavioural thermoregulatory devices with dragonflies i.e.

sun-, ground- and rock-basking, shivering and wind avoidance (CLENCH, 1966). This provides opportunity for a broader approach to ecological landscaping for the conservation of both insect groups.

MICROHABITAT PREFERENCES, ROCK- AND GROUND-BASKING

Some species basked on rocks, others on the ground, and some on both. These thermoregulatory activities exploit high substrate temperatures and unique conditions associated with boundary layers, i.e. still layers of air in contact with broad surfaces (GEIGER, 1971; MAY, 1978). The air of the boundary layer adheres tightly to the substrate, is free from turbulence, and heat transfer within the layer occurs only by physical conduction. The Ta of this 1-10 mm thick layer is, thus, often substantially higher than Ta above it (YOSHINO, 1975). Air transports temperature changes far more easily than rock or soil which, especially if dark in colour, retain heat for longer (GEIGER, 1971). The light-coloured concrete slab in the hollow was not basked on as extensively as the ochre-brown natural rock. Suitable substrates are generally scarce in natural landscapes and if ecological landscaping is planned, consideration should be given to the albedo and heat-absorbing properties of materials used (e.g. rock, soil).

By fine postural adjustment, such as raising and lowering of the thorax and abdomen, basking dragonflies may manipulate the relative extents of conduction, convection and radiation received from the rock surface and achieve a high degree of temperature control.

The duration of rock-basking on each occasion was highly variable, and appeared to be dependent on Ta and Tr as it occurred within a constant narrow range. Basking insects must leave their perch before their Tth drops below that able to initiate and sustain flight (VOGT & HEINDRICH, 1982). MAY (1976) found that the minimum Ta that could sustain flight in the laboratory was 21.3 ± 1.6°C (± 1 S.E.), although light-intensity and time of day also play a role (CORBET, 1983). This relates well with Tr's determined after dragonflies left their rock-perches, presuming that Tth approaches Tr as shown by TRACY et al. (1979). If Tth does drop too far the dragonfly may elevate Tth by low-amplitude wing vibrations, i.e. wing-whirring (MAY, 1976) as occurred in the two *O. caffrum* males. *O. caffrum* is a percher and an ectothermic species although it intermittently resorts to this endothermic means of Tb control (MAY, 1991). It appears, however, that endothermy is used as a last resort in comparatively small species, such as *O. caffrum*, due to the high energy expense of this method (MAY, 1978). Rock-basking here, is different from the behaviour of many gomphids, e.g. *Paragomphus cognatus* (Ramb.). They use rocks as foraging perches, particularly in the centre of streams, and flatten themselves against the rock-surface to escape predation by swooping birds.

Differences between male and female choice of perch site have been recorded, e.g. *Erythemis plebeja* females were observed to most often perch at the forest edge, whereas males tended to perch in sunny, exposed spots (MAY, 1978). The phenomenon observed in *O. caffrum* males and females is not easily explained. The sexually dimorphic colouring in this species makes the dull orange-brown female virtually indiscernible, at least to the human eye, when perching on the gravel substrate of the hollow (less so on the rock surface), whereas the bright blue males are highly conspicuous against both the rock surface and gravel substrate. During this study there was never any attempt, by bird or reptile predators, to prey on basking individuals. Lizards were ubiquitous in the area and often shared perches with the dragonflies, yet never disturbed them. If camouflage is an explanation for different basking-site preferences in the two sexes of *O. caffrum*, it would apply only to the female.

ADAPTIVE SIGNIFICANCE OF OBSERVED BEHAVIOUR

The basking activity between 14h00 and 18h00 is a long time in the daily activity period of these Anisoptera, during which no reproductive behaviour, and negligbile foraging, occur. Although CORBET (1980) reports that predation of adult dragonflies is generally very low, aggregations of such large, often conspicuously coloured insects could be expected to attract predators. The rock--baskers, particularly, were fully exposed on the rocks to potential predation or disturbance. What reasons are there, then, for prolonging the onset of roosting, or settling in a shaded area, under conditions of dropping temperature, when surrounding zones are still exposed to late-afternoon sunshine? Certain advantages are to be gained by maintaining Tth high enough to allow flight for as long as possible. MAY (1977) proposed that the physiological advantages of maintaining Tb above a certain threshold is to extend the activity period.

Absence of aggression was likely as a result of ambient temperature being too low for reproductive behaviour. These thermoregulatory behaviours do not appear to benefit mating success or oviposition rate. In reproductive individuals, however, adult fecundity may be increased by prolonging periods of spermatogenesis and accelerating egg maturation with maintenance of Tb above a certain level (MAY, 1979; DAVENPORT, 1985; MAY, 1991). Aggregations in thermally favourable environments may also function secondarily as leks.

MAY (1979) suggests that crepuscular activity may occur to take advantage of unexploited food sources, e.g. midge swarms which are common at this time of day. Extension of the foraging period may be an influencing factor in this assemblage if foraging occurs between the time of leaving the hollow and the onset of roosting.

Predator avoidance, by retaining the ability for quick and agile flight until dark, seems a logical benefit and could be a selective force, although observations do not support this, and congregation in such numbers would appear rather to increase the predation risk.

Numerous other selective pressures for prolonged thermoregulation have been suggested, i.e. heightened metabolic rate (SHELLY, 1982), increased foraging rate with higher Tb (MAY, 1991), temperature effects on the nervous system and visual acuity (MAY, 1979). In reptiles, high Tb speed digestion (DAVENPORT, 1985). This behaviour may also enable dragonflies to reach, or search for, suitable roosting sites.

Within the hollow *O. caffrum* and *C. erythraea* showed distinct separation of thermal microhabitat, the former basking on rock or ground, and the latter perching in high numbers low in the vegetation. HEATH et al. (1971) report that niche specialization, in order to avoid competition, can and does result from particular requirements in the form of thermal preferenda (temperature range within which congregation of individuals occurs) (REYNOLDS & CASTERLIN, 1979; SHELLY, 1982). The variety of microhabitats here was differentially important to the species present.

Temperature tolerances and responses may be an adaptation to a particular thermal environment and to habitat (MAY, 1976; 1991).. Perchers in Maine (U.S.A.) had flight-threshold limits of 6-8°C lower than similar species from Florida and Panama (VOGT & HEINDRICH, 1983). MAY (1976) emphasizes that thermoregulatory responses are of a facultative nature, dependent on the peculiarities of climate experienced by every population, and that dragonflies characteristically behave in an opportunistic manner. This plasticity of behaviour is seen as one of the features contributing to the success and survival of dragonflies through geological time (CORBET, 1983).

CONSERVATION DIRECTIVES

The anisopteran assemblage studied here has the thermoregulatory ability to exploit facultatively a unique set of landscape features available to it. Four thermally attractive microhabitats were distinguished. The protected environment of the hollow provides wind shelter and high-temperature thermal layers near the ground. Low vegetation, rock surfaces and open gravel and sand substrates are also exploited for their thermal properties. Provision of these elements in a formally designed landscape, in the vicinity of water, would encourage a number of Anisoptera. Ecological landscapers and insect conservationists should be aware of the importance of such small, seemingly unimportant, landscape elements like the hollow, when considering alterations to pristine landscape or the creation of dragonfly reserves in urban environments.

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