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Shade Alone Reduces Adult Dragonfly (Odonata: Libellulidae) Abundance

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Abstract We demonstrate that physical habitat conditions influence adult dragonfly (Odonata: Anisoptera) riparian site selection. In naturally treeless riparian areas of South Africa, invasive trees create shade and reduce native vegetation. We hypothesized that most breeding odonates select riparian areas (1) without shade, and (2) with high density and variety of understory perch structures. In two experiments at reservoir shorelines, we varied shade and perch structures. Dragonfly abundances (predominantly *Trithemis* species) were lower at sites with high (75%) or moderate (55%) shade cover than at sites with no shade, and lower at bare sand sites than sites containing stick perches. Perch density and variety (variety of heights and diameters) did not affect dragonfly abundance. These results indicate that shade alone directly reduces dragonfly habitat selection, isolating one aspect of habitat change that can alter insect behaviors.

Keywords Odonata · *Trithemis* · habitat structure · shade · riparian vegetation · habitat selection

Introduction

Insects and other animals respond behaviorally to physical habitat conditions, including those created by tree canopies. Light interception by trees affects conditions

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for thermoregulation and visibility (Endler 1993; Thery 2001). Tree canopies may also influence insect behavior indirectly via effects on understory vegetation and prey composition. Changes to canopy structure from logging and other disturbances can thus strongly influence insect habitat use. Invasion by non-native plants is a disturbance that increasingly affects insect behavior through alteration of physical habitat structure (Samways et al. 1996; Gratton and Denno 2005).

In South Africa, most riparian corridors had no indigenous trees and were open until Australian black wattle (*Acacia mearnsii*) and long-leaved wattle (*A. longifolia*) invaded and formed dense canopies (Gorgens and van Wilgen 2004). Numerous plants and insects are likely sensitive to the shading effects of invasive *Acacia* (Breytenbach 1986; Richardson et al. 1989; Samways 2006), but experimental research is needed to isolate direct effects of shade. Our field experiments independently test effects of shade intensity and perch availability on South African adult dragonfly (suborder Anisoptera) riparian site use. Understanding which components of habitat disturbance are most influential for odonates can inform conservation strategies.

Observational studies suggest that many adult Odonata (dragonfly and damselfly) species avoid shaded areas (Pezalla 1979; McKinnon and May 1994; Chwala and Waringer 1996; Clark and Samways 1996; Painter 1998; Kinvig and Samways 2000; Samways and Taylor 2004; Samways et al. 2005; Ward and Mill 2005). Their behavior may reflect thermoregulation requirements. Insects and other ectothermic animals are particularly sensitive to the variation in microclimates produced by vegetation (e.g., May 1976; McGeoch and Samways 1991; Downes and Shine 1998; Arnan et al. 2007; Valentine et al. 2007). Lighting can also play an important role in habitat selection (e.g., Davies 1978; McCall and Primack 1992; Grundel et al. 1998; Bernath et al. 2002; De Cauwer et al. 2006; Reinhardt 2006) because insects that fly during the day orient almost entirely based on visual cues (Lehrer 1994; Dafni et al. 1997; Egelhaaf and Kern 2002; Olberg et al. 2005).

Odonate species in the "percher" behavioral guild may require riparian understory vegetation because the adults guard breeding territories, thermoregulate, and watch for prey from plant perches (Corbet 1999). Previous studies indicate greatest abundances of adult dragonflies in areas with tall wetland plants (McKinnon and May 1994; Ueda 1994; Clark and Samways 1996; De Marco and Resende 2004; Foote and Hornung 2005; Ward and Mill 2005), perhaps because they serve as perch structures. A few researchers have added artificial stick perches to their study sites to manipulate dragonfly distributions for studies of mating or feeding behavior (Wolf and Waltz 1988; Rehfeldt 1990; Baird and May 1997; May and Baird 2002), but no previous research has specifically tested effects of perch stem density on odonate habitat selection. We hypothesized that riparian sites with higher densities of perch structures (sticks we erected in the sand) would have greater odonate abundances than sites with fewer or no perch structures.

The distribution of plant heights or forms (structural variety) may change independently of plant density. Odonata likely respond more to structural variety than to particular plant species (Buchwald 1992; Corbet 1999; Foote and Hornung 2005). Taller perch structures can facilitate territory guarding, so perching height is often proportional to body size (Corbet 1999; De Marco and Resende 2004). Odonate species (namely damselflies, suborder Zygoptera) also select perch structures based on stem diameter (Askew 1982; Rouquette and Thompson 2007).

Thus, we expected that sites with a variety of stick diameters and heights support higher dragonfly species richness and abundance than sites with uniform sticks.

In addition, we hypothesized that perch-stick location relative to the water's edge affects Odonata behavior. Specifically, we expected that territorial male dragonflies would select perch-sticks closest to the water, perhaps to intercept females en route to oviposition sites (Van Buskirk 1986; Switzer and Walters 1999). Testing whether odonates use structures farther from the water can inform land managers seeking to establish riparian buffer widths and manage for wildlife diversity. Thus our research questions were: 1) Do dragonflies avoid shaded zones? and 2) Do density, variety, or position of perch structures affect dragonfly site use?

Materials and Methods

Study Area

Separate shade and perch-stick experiments were conducted at two small reservoirs with little shoreline vegetation on Vergelegen Estate, Western Cape, South Africa. Both reservoirs receive water from the Hottentots-Holland Mountains, and each is ~2 ha in area. By the end of the dry summer, when field experiments began, water levels in the reservoirs had dropped so that bare shorelines about 15 m wide were exposed around the margins of both reservoirs. These shorelines lacked tall vegetation, providing relatively homogeneous field sites where we could experimentally isolate the structural variables of interest: shade levels, perch-stick density, perch-stick variety, and perch-stick distance from water. The adjacent aquatic habitats were also relatively homogeneous, with gently sloped littoral areas composed of sand and clay and no emergent plants.

Field Methods

We established twenty shade plots, with four shade levels replicated randomly within five complete blocks. Distances of 8 to 20 m separated the blocks. All treatment plots (2.8×2.8 m each) were separated by at least 5 m, and were 1 m away from the water's edge (although the water level receded to a distance of about 3 m from the shade treatments during the study period). We suspended three types of commercial plant nursery shade cloth 2 m off the ground with wooden poles (about 10 cm in diameter) and nylon ropes. We chose this height because it was above normal anisopteran flight routes. Shade cloths were solid green or black and provided three levels of sunlight interference: 30%, 55% and 75% shade. Control treatments, which we refer to as 0% shade, were set up with the same pole and rope structures, but no cloth. Shade levels were verified using a standard light meter to quantify percent of full sunlight available under each shade cloth treatment at approximately the same time of day for all treatments. We measured light levels at a typical odonate perching height of 20 cm above the ground. Nearby invasive *Acacia* trees created 96–97% shade at the same height. To standardize structures and facilitate observations in the plots, we trimmed any vegetation present, and erected 16 sticks (2 per m^2) of equivalent sizes (6–10 mm diameter; 0.4–0.5 m tall) in a grid pattern beneath the shade cloth.

At the other reservoir, we used regular grids of *Eucalyptus* sticks to mimic two structural attributes of understory shoreline vegetation: stem variety and stem density. We used a fully crossed randomized complete block design with two stick density x two stick variety treatments, plus a control treatment having no stems. These five treatments were each replicated across four complete blocks; treatments were assigned randomly within each block. We separated each (3 × 2.5 m) treatment plot by 5 m and each block by 5–10 m. The high-density stick treatments contained 30 sticks (4 per m^2), and the low-density treatments contained 9 sticks (1.2 per m^2). We also created low stick variety at half of the treatments by using sticks of all the same diameter and height, and high stick variety at the other half of treatments by including an even mixture within plots of ‘tall thin’, ‘tall stout’, ‘short thin’, and ‘short stout’ sticks. The ‘thin’ sticks were 2–6 mm in diameter, while ‘stout’ sticks were 15–20 mm in diameter. All sticks were clearly taller than any other vegetation emerging in the plots: ‘tall’ sticks were 0.6 m high, and ‘short’ sticks were about 0.2 m high. Average odonate perch heights vary between 0 and 0.75 m (May 1976; Nomakuchi 1992; McKinnon and May 1994; Reinhardt 1999). For the low perch variety treatments (where all sticks within a plot were of the same size), each block contained a different stick size (from the four height and diameter combinations).

We observed dragonflies in all shade treatments for 10-minute periods and perch-stick treatments for 5-minute periods. Two observers collected data only on 11 calm, sunny days during February – April 2005 between 9h45 and 15h45, the hours when odonates are most active. Although the shadow of shadecloths moved somewhat throughout the course of the day, we observed odonates only within the shaded portions of each plot. We observed the same plot portions (measurable from the regular grid of stick perches) for the same time period within each location block. Observation periods began one minute after the observers became situated in front of each plot. Observers sat on shore 2 m inland from the edge of each plot, at the center of each plot’s shoreline width. We saw no evidence of altered dragonfly behaviors when observers were at least a meter away from perch locations. Although changing weather conditions prevented us from observing all location blocks on each of the 11 days, we completed observations on all treatments within a block each day (for both experiments).

During each observation period, we recorded the number and species of dragonflies perching in the plot, investigating the plot (flying slowly), and passing (flying quickly) through the plot. We also recorded the number of dragonflies in the plot at the instant when a timer signaled the end of the observation period, which we used as a measure of dragonfly relative abundance per plot. Abundance estimates were mainly comprised of individuals perching within treatments. Size of the plots enabled observers to count all anisopterans in each plot during a single glance. Species present were easy to distinguish on the wing. At the perch-stick experiment, we also noted where perching occurred from one of two distance-from-water categories (1–2.5 m or 2.5–4 m inland).

Statistical Methods

Single-factor randomized-block Analysis of Variance (ANOVA) tests were used to compare means of six response variables among shade treatments (an ordered variable): 1) Anisoptera relative abundance; 2) number of Anisoptera slow (investigative) flights divided by total number of Anisoptera entries in the plot; 3) Anisoptera perch selectivity (number perching divided by total number of Anisoptera entries in the plot); 4) *Trithemis dorsalis* perch selectivity; 5) *T. arteriosa* perch selectivity; and 6) proportion of perching Anisoptera on the ground. Based on Bonferroni corrections for conducting six separate tests, we assessed significance at $p<0.008$. We used the sums of response variables across all 11 observation days to compare treatments ($n=20$ for both perch and shade experiments). Response variables were square-root transformed when necessary to fulfill normality and homoscedasticity assumptions. Using Tukey's Honest Significant Difference (HSD) tests, we conducted post-hoc pairwise comparisons among treatment means.

We used two-factor randomized-block ANOVAs to compare means of six response variables among the two perch-stick variety and two perch-stick density treatments: 1) Anisoptera species richness; 2) Anisoptera relative abundance; 3) number of Anisoptera slow (investigative) flights divided by total number of Anisoptera entries in the plot; 4) Anisoptera perch selectivity (number perching divided by total number of Anisoptera entries in the plot); 5) *T. dorsalis* perch selectivity; and 6) *T. arteriosa* perch selectivity. With Bonferroni corrections, the rejection criterion was $p<0.008$. We subsequently compared response variables among the three perch-stick density treatments (including the control) with one-way blocked ANOVAs. To test whether dragonflies perched more than expected at random on the row of sticks closest to the water, we used a two-sided t-test ($n=20$). All analyses were conducted using R 2.2.0 software (R Development Core Team, 2005, Vienna, Austria).

Results

Anisoptera species recorded within the plots included three Libellulidae (*Trithemis dorsalis, T. arteriosa, Pantala flavescens)*, one Aeshnidae (*Anax imperator*), and one Gomphidae (*Paragomphus* sp.). All of these species, except *P. flavescens*, are known to oviposit in the reservoirs (M. Samways, personal observation). One zygopteran species (*Africallagma glaucum*) was also occasionally observed in the plots, but was not included in the dataset because its locations proved too difficult to track reliably in conjunction with anisopterans. The two *Trithemis* species were by far the most abundant odonates within the experimental plots (77 and 95% of individuals perching in shade and perch experiment plots, respectively). Plot entries by members of the flier behavioral guild (*P. flavescens* and *A. imperator*) did not differ among shade treatments ($F_{3,12}=0.9$, $p>0.1$). We found no apparent trends in species abundances or behaviors across the study period.

Anisoptera mean perch selection decreased from 0.5 to 0 perches per plot entry as shade cover increased from 0% to 75% shade ($F_{3,\ 12}=13.7$, $p=0.0004$; Fig. 1). Specifically, mean perch selection for both species tested was higher at the plots with no or low (30%) shade than at the 75% shade plots (*T. arteriosa:* $F_{3,\ 12}=12.9$, $p=0.0005$; *T. dorsalis:* $F_{3,\ 12}=14.9$, $p=0.0002$; pairwise differences based on Tukey's HSD tests with $p<0.05$). Mean anisopteran abundances followed the same pattern ($F_{3,\ 12}=5.6$, $p=0.01$), with greater significance when we excluded abundance

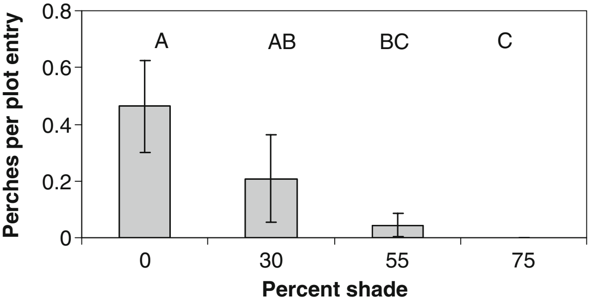

Fig. 1 Mean count of perching Anisoptera (corrected by the total number of anisopteran entries) within each shade treatment (n=20). *Different letters* indicate significant differences based on Tukey's honest significant difference tests ($p<0.05$). *Error bars* represent two standard errors above the mean and two standard errors below the mean.

estimates from an outlier zero-shade plot that had no odonates present during the relative abundance counts ($F_{3,\ 11}=24.7$, $p<0.0001$). Neither investigative (slow) flights nor proportion of perching Anisoptera on the ground differed by shade treatment ($p>0.1$).

Based on the perch-stick experiment two-way ANOVA, mean Anisoptera abundance, richness, investigative flights, and perch selection did not differ with perch variety or density. The one-way ANOVA comparing three stick densities revealed that mean Anisoptera abundance was 2.5 to 2.7 times higher at the stick treatments than at control plots without sticks ($F_{2,\ 14}=6.8$, $p=0.009$), with no significant differences between plots with high and low stick densities (Fig. 2). Although the differences were not significant (acknowledging Bonferroni corrections), Anisoptera perch selection followed the same pattern, with the mean perches per entry 1.6 times higher at stick treatments than at the control plots ($F_{2,\ 14}=6.3$, $p=0.01$). By species, perch selections were not significantly lower at control plots than at plots with high or low stick densities (*T. dorsalis* $p=0.02$; *T. arteriosa* $p=0.1$). The proportion of ground perches per plot entry ranged from 0.08 (at a high stick density plot) to 0.47 (at a control plot). Based on perch location data across all five treatments, dragonflies perched more frequently (63% of observed perches) in the half of the treatment closest to water ($t=90.8$, $p<0.0001$).

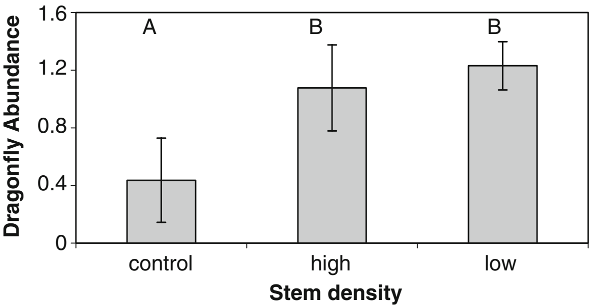

Fig. 2 Mean Anisoptera abundance associated with three types of stem treatments. The control was without sticks, while high and low stem density treatments had 30 and nine sticks erected, respectively. *Different letters* indicate significant differences based on Tukey's Honest Significant Difference tests ($p<0.05$); *error bars* show two standard errors both above and below the mean.

Discussion

Results from the shade experiment provide strong evidence for shade avoidance behavior by the two most abundant anisopterans around the reservoirs. The three shade treatments had identical structures other than cloth weave density, although the control treatment lacked shade cloth completely. Under the assumption that presence of shadecloth could inhibit dragonflies from entering plots rather than their decision to perch there, we considered whether dragonflies responded adversely to the artificial screen structures rather than shade alone. The perch selection response adjusts for potential alteration of behavior by screen structures because it standardizes by the total number of entries into a plot. Notably, we recorded lower perch selection at the 75% shade treatment than at the 30% shade treatment, which had no differences in structure. After controlling for effects of structure *per se*, we thus conclude that shade alone can have a significant inhibitory effect on the behavior of these species.

Whether shade limits prey availability, mate attraction, hunting effectiveness, or thermoregulation remains to be tested. Vegetation structure can simultaneously influence trophic interactions through several of these mechanisms (e.g., Coll et al. 1997). Prey availability seems less likely to control the distribution of adult odonates around water bodies because they are mobile, generalist predators. Based on rapid flight paths following shade boundaries (Reinhardt 2006), odonates may distinguish shade boundaries by sight rather than solely by temperature.

Presence of perch-sticks increased odonate abundances, but contrary to our hypotheses, the density, size, height, and heterogeneity of perch-sticks set up in unshaded areas had little effect on odonate abundances. Examination of a broader range of stem varieties, though, may reveal additional odonate perch selection preferences. Future research on how riparian stem densities affect odonates should examine habitat differences between zero and very low stem densities because aggressive interactions among males generally lead to low densities of perching males. The only measurable perch preferences we observed were for sticks closest to the water. Preference for perch sites within 1 m of the water's edge concurs with previous odonate behavior studies (Ward and Mill 2005). Proximity to suitable oviposition areas likely explains this perching behavior for male dragonflies (Van Buskirk 1986), although prey density gradients could also be investigated with additional field studies. Our results suggest that understory perch structures only affect odonate habitat selection when they are completely absent.

Identification of the physical habitat conditions that affect insect behavior and distributions can inform conservation strategies. Scarcity of threatened populations often necessitates behavioral research on related species. Because body size and pigmentation likely influence thermoregulation behavior (May 1976; De Marco and Resende 2002), other Odonata species with similar morphologies may exhibit similar responses to shade.

Knowledge that shade affects odonates directly, rather than via reductions of other habitat structures, suggests that removal of alien tree canopies will enhance populations of indigenous dragonflies more than efforts to provide understory vegetation. The South African national Working for Water Programme, devoted to removal of alien riparian trees, has improved wildlife habitat by returning many riparian areas to sunlit conditions (Samways and Grant 2006). Although selection of appropriate larval habitat also influences adult dragonfly behavior (e.g., Michiels and Dhondt 1990; De Marco and Resende 2004), we demonstrated that the riparian forest canopy and associated disturbances can affect riparian site use by adult dragonflies.

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