Odonatologica 33(2): 129-146 *June 1, 2004*

ADULT ZYGOPTERA OF KIBALE NATIONAL PARK, UGANDA: HABITAT ASSOCIATIONS AND SEASONAL OCCURRENCE

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Received February 22, 2003 / Revised and Accepted November 3, 2003

In this study, a 10-month survey of four aquatic sites in Kibale National Park, Uganda was used to quantify seasonal and spatial variation in both limnological features of the sites and adult damselfly assemblage structure. Of the 4 limnological characters measured dissolved oxygen was the most variable among sites, ranging from an average of 1.01 mg l^{-1} in the interior of the Rwembaita Swamp (a papyrus-dominated wetland) to 6.71 mg l^{-1} in an inflowing tributary of the swamp. Species richness was similar among sites and did not correlate with dissolved oxygen concentration. However, site was a significant predictor of occurrence for some spp. This suggests that site effects are important, and that a combination of site-specific environmental characters may underlie the observed distributional patterns. Seasonal fluctuation in rainfall was not a good predictor of Zygoptera activity. Several spp. were active in both the wet and dry seasons. Surprisingly, adult *Proischnura subfurcatum* were detected year-round in the hypoxic waters of the Rwembaita (papyrus) Swamp and did not occur at any other sites in the larval or adult phase, suggesting that this sp. is a swamp specialist.

INTRODUCTION

A central theme of ecology is understanding patterns in the distribution and abundance of organisms and the selective pressures that underlie these patterns. Clearly, the abiotic environment has a major influence on the ecology of organisms (WOLANSKI & GERETA, 2001). Abiotic factors may affect growth, reproduction, and survivorship, thereby influencing patterns of distribution and habitat use (FLEMER et al., 1999). For aquatic insects, important abiotic conditions include water temperature (ARTHUR et al., 1982; GILLOOLY & DODOSON, 2000), dissolved oxygen concentration (DAVIS,

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1975; JACOB et al., 1984), pH (HALL & IDE, 1987; ROUSCH et al., 1997; COURTNEY, 1998), flow (FEMINELLA, 1996; WELLNITZ, 2001), and conductivity (CANNINGS & CANNINGS, 1987) since it is reflective of total dissolved ion concentrations (ALLAN, 1995). Many of these factors vary among aquatic habitats (i.e., streams, lakes, swamps, etc.) and may fluctuate daily (HUBERTZ & CAHOON, 1999, FENCHEL, 2000) or seasonally (LAHR et al., 1999; BORSUK et al., 2001). The role these factors play in shaping habitat quality may explain patterns of geographic distribution, habitat associations, and seasonal variation of some aquatic insects.

Zygoptera have a two-stage life history pattern, and characteristics of both aquatic and terrestrial environments shape the ecology of this group. With few exceptions (WILLIAMS, 1936; KELTS, 1979; WINSTANLEY, 1983; GARRISON & MUZÓN, 1995) damselflies inhabit fresh waters in egg and larval stages prior to their metamorphosis into a winged terrestrial adult. Thus, the aquatic environment affects egg and larval stages directly and affects adults indirectly due to selective pressures to choose favorable sites for egg and larval development. For example, odonate eggs and larvae may suffer high mortality, or slow or impaired development when exposed to unfavorable conditions such as desiccation (BENNETT & MILL, 1995) or sub-optimal temperatures (LAWTON, 1970; HALVERSON, 1983; LUTZ & ROGERS, 1991; HAWKING & NEW, 1995). Because these conditions may vary seasonally, adult activity and breeding may be timed to coincide with optimal environmental conditions in the larval habitat.

Patterns of adult activity, breeding, and larval development in odonate species differ markedly between temperate and tropical regions. In temperate regions, larval periods (time between hatching and emergence) tend to be longer than in tropical species (CORBET, 1980; KUMAR, 1976). Most temperate damselflies require 1 to 2 years for a complete generation (CORBET, 1999), and some may take more than 4-5 years to complete larval development (NORLING, 1975; UBUKATA, 1980). In contrast, some tropical damselflies have three or more generations per year (KUMAR, 1976). Because growth in damselflies is temperature-dependent (PROCTER, 1973), differences in larval periods between temperate and tropical regions are thought to reflect latitudinal variation in climatic conditions, specifically temperature (CORBET, 1999). Furthermore, broad-scale zoogeographical patterns in species distributions also reflect isoclines of temperature variation. In temperate regions, seasonal fluctuations in photoperiod are also very important to the ecology of larval dragonflies and damselflies, particularly as cues for timing in larval development (CORBET, 1955; PROCTER, 1973). In the tropics, where seasonal variations in temperature and photoperiod are more modest, patterns of rainfall seem to be more important in controlling seasonal patterns of larval development (KUMAR, 1972), though temperature ultimately affects developmental rate (KUMAR, 1976).

While tropical systems are known to support impressively diverse insect faunas (ERWIN, 1982), the majority of these groups are poorly understood, and studies linking seasonal variation in abiotic conditions to patterns of zygopteran distribution and abundance are limited in number and geographic scope. In particular, there are few studies linking distribution of larval damselflies with characteristics of the aquatic environment in Africa. In some regions this may be attributed to the lack of larval taxonomy. For example, in East Africa, few zygopteran larvae have been linked to adult forms. This taxonomic constraint limits our ability to develop predictive models of damselfly larval distribution based on aquatic habitat characters. However, habitat relationships may be cautiously inferred based on distribution and behavior of adults, because seasonal patterns of adult activity often reflect patterns in the timing of larval emergence, adult longevity, and emigration (CORBET, 1999). In this study, we use this tool to understand distribution patterns and assemblage structure in an Afrotropical damselfly community.

In general, the ecology of East African damselflies has not been extensively described, and patterns of habitat association and seasonal variation remain largely unknown. However, recent distributional surveys (CLAUSNITZER, 2001) in East Africa have provided preliminary data for diversity hot spots in the region (e.g., wetlands and swamp forests). Forty-seven odonate species are found in Kibale National Park, Uganda and the surrounding areas (DIJKSTRA & DINGEMANSE, 2000). These preliminary surveys suggested that damselfly assemblage structure varies among habitats. These data in conjunction with preliminary data collected in 1999 (C.K. Apodaca) raised the possibility that the papyrus swamps of Kibale National Park may host a unique damselfly assemblage. These swamps provide challenging abiotic conditions because they are characterized by chronically low oxygen throughout most of the year (CHAPMAN et al., 2000). The objective of this study was to describe damselfly species assemblages across four aquatic sites in Kibale National Park, Uganda that differ in basic limnological features to detect links between adult assemblage structure and the habitat characteristics of the aquatic environment.

In this paper, we present results from a 10-month survey of adult damselflies at four sites in Kibale National Park. Concurrently with the surveys, we measured conductivity, dissolved oxygen, pH, rainfall, and water temperature at these sites. Our specific objectives were to (1) describe species assemblages at four aquatic sites (two swamp and two stream sites), (2) describe seasonal variation in adult damselfly occurrence at these sites, and (3) provide preliminary information on seasonal variation in breeding behavior of adults. We predicted (1) the use of swamp habitats by damselflies follows a seasonal pattern, with most activity occurring in the wet season, (2) many species fit into community assemblages that are specific to certain habitats, and (3) the presence of adult damselflies correlates with limnological characteristics of the larval environment.

STUDY AREA AND METHODS

STUDY AREA. – Kibale National Park (0°13'-0°41'N and 30°19'-30°32'E) is located in western Uganda near the foothills of the Rwenzori Mountains. Approximately 58% of Kibale is characterized by semi-deciduous and evergreen forest (CHAPMAN & LAMBERT, 2000), with canopy height ranging from 25 to 30 m (BUTYNSKI, 1990). The remainder of the park is secondary forest (19%), grassland (14.5%), wetlands (2%), woodland (6%), and plantations (1%; CHAPMAN & LAMBERT, 2000). Kibale National Park receives approximately 1749 mm of rainfall annually (1990-2001) that peaks during two rainy seasons (L.J. Chapman

& C.A. Chapman, unpublished data) with most rain falling March through May and September through November. However, the onset, duration, and magnitude of the rains varies among years. The mean daily minimum temperature is 15.5 °C; and the mean daily maximum temperature is 23.8 °C (1990-2001).

SITE DESCRIPTIONS AND LIMNOLOGICAL SAMPLING. – We quantified seasonal occurrence of adult damselflies and characterized seasonal fluctuations in four limnological parameters at two intermittent forest streams (Mikana Stream and Inlet Stream East), a large papyrus swamp (the Rwembaita Swamp), and a permanently flowing swamp stream (Njuguta Swamp Stream) in Kibale National Park (Fig. 1).

Four limnological characters (conductivity, dissolved oxygen, pH, and water temperature) were sampled bi-monthly at the four sites where the seasonal distribution of adult damselflies was monitored. Dissolved oxygen (mg l^{-1}) and water temperature (°C) were measured with a Yellow Springs Instruments (YSI) meter (Model 95). Conductivity (μS cm^{-1}) was measured with a YSI Model 30 meter, and a chek-mite pH sensor was used to measure pH. Rainfall data were recorded at the Makerere University Biological Field Station (Fig. 2), located approximately 3 km from the Rwembaita Swamp. Water current was ranked on a scale from 0 to 3 (0 = no current, 1 = visible but low flow, 2 = fast flow with little water perturbation, 3 = fast flow with water perturbation). Detailed descriptions of each study site are provided below.

INLET STREAM EAST. – This stream flows through swamp forest and then through mature secondary forest before entering the swamp. The study site was a 220-m stretch of the stream just before its confluence with the papyrus swamp. During the period of study ISE averaged 25 cm in depth and 1 (on a scale of 0 to 3) in flow. Dissolved oxygen and water temperature were measured at four stations at this site, and conductivity and pH were measured from water samples taken at three of these stations. Collection of damselflies occurred over the 220-m study stretch.

MIKANA STREAM. – This intermittent stream is 1,400 m long and passes through mature secondary forest before flowing into the Rwembaita Swamp. This stream is the largest tributary of the swamp, aver-

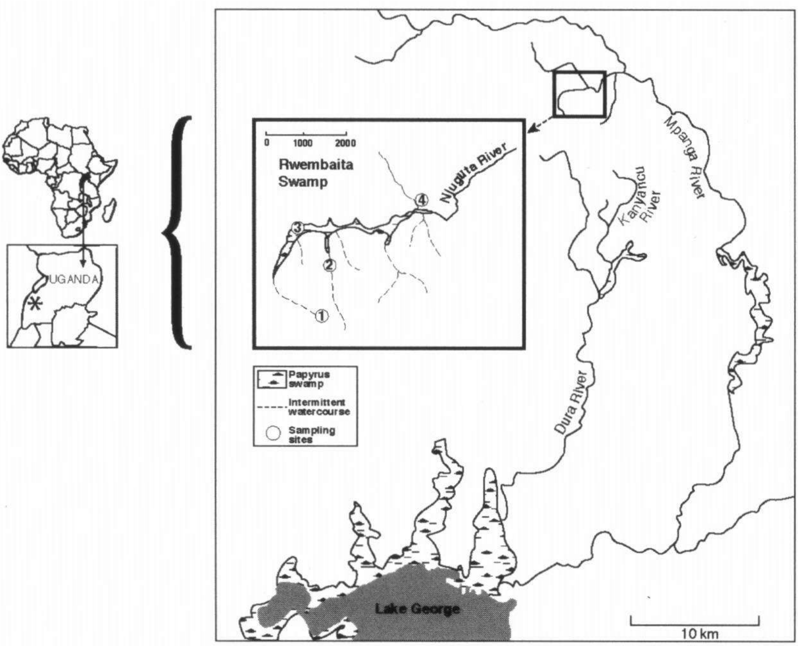

Fig. 1. Map of the study area in Kibale National Park, Uganda, East Africa. Site 1: Mikana Stream; – Site 2: Inlet Stream East; – Site 3: Rwembaita Swamp; – Site 4: Njuguta Swamp Stream.

aging approximately 1 m in width (CHAPMAN et al., 2000). Dissolved oxygen and water temperature were measured at 13 sampling stations distributed along a 275 m reach starting at the Census Road bridge and extending downstream. During the study period these sampling stations averaged 17 cm in depth and 0.8 in flow (on scale of 0 to 3). Conductivity and pH were measured from three water samples taken at the bridge and 205 m and 255 m downstream. For each sampling period average water temperature (n = 13), dissolved oxygen (n = 13), pH (n = 3), and conductivity (n = 3) were used to characterize the site. Collection of adult damselflies occurred from the bridge to 275 m downstream.

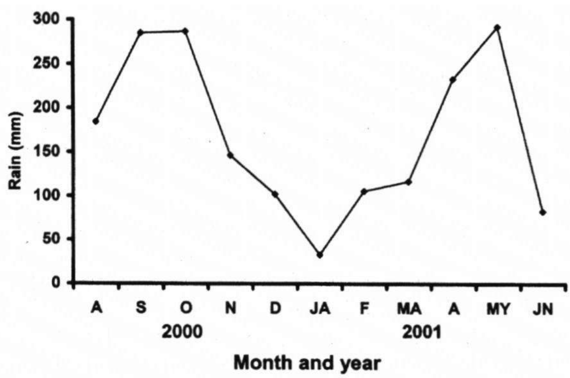

Fig. 2. Monthly rainfall (mm) measured at the Makerere Biological Field Station, Uganda throughout the study period (August 2000 to June 2001).

NJUGUTA SWAMP STREAM. – In the northern region of Kibale National Park, the hypoxic water from the Rwembaita Swamp flows into the well-oxygenated Njuguta River by way of this short connecting stream (approximately 3 m in average width). Upper reaches of this stream are partially shaded by overhanging trees and vegetation. All limnological characters were measured at four stations spaced 20 m apart between 20 to 80 m upstream of the Njuguta River confluence. For each sampling period, the average water temperature, dissolved oxygen, pH, and conductivity of the four stations were used to characterize the site. During the study period these sampling stations averaged 129 cm in depth and 1.3 (on a scale between 0 and 3) in flow. Adult damselflies were collected from the point where the swamp stream flows into the Njuguta River up to 100 m upstream of the confluence.

RWEMBAITA SWAMP. – This large papyrus-dominated swamp is fed by several forest streams, but during drier months of the year the swamp consists mostly of large stagnant pools with a few channels of running water. During the wet season, the influx of running ground water transforms the interior swamp to a network of flowing channels. Limnological characters were measured in pools of the interior swamp at six stations. For each sampling period, the average water temperature, dissolved oxygen, pH, and conductivity of the six stations were used to characterize the site. During the study period, these sampling stations averaged 55 cm in depth and 0.3 (on a scale of 0 to 3) in flow. Adult damselflies were collected near stagnant pools and along channels of flowing swamp water. The collection area extended about 100 m into the interior swamp from the swamp bridge.

COLLECTION AND PRESERVATION OF ADULT DAMSELFLIES. – Adult damselflies were collected bi-monthly at the four study sites within Kibale National Park between August 2000 and July 2001. Two people with aerial nets visited each site and actively searched for adult damselflies for approximately 1 h. While collecting, the observers actively searched for females and males of all species present. Captured damselflies were immediately preserved in 95% ethanol alcohol and subsequently identified with the aid of a dichotomous key (V. Clausnitzer, unpublished). We tried to consistently collect adults during the warmest time in the day. For each sampling period, we recorded presence or absence of males, females, and pairs in tandem for each species.

STATISTICAL ANALYSES. – For all analyses, samples were categorized as occurring in either the wet or dry season. The dry season (November to March, and June) was defined as months when rainfall was below the median, and the wet season (August to October and April and May) included all months when rainfall was above the median. Analysis of variance (ANOVA) was used to compare means of wet and dry season measures for conductivity, dissolved oxygen, pH, and water temperature among the four sites. When means differed among sites, we used Scheffe's post-hoc test to perform multiple comparisons. Pearson correlation was used to detect relationships between limnological characters over the study period within sites (n = 22 per site). Spearman rank correlation was used to detect relationships among limnological characters across the four sites.

To compare the probability of adult damselfly occurrence among sites and between seasons, we used binary logistic regression. For each species, we modeled the probability of occurrence during a sampling period as a function of site (nominal, four sites), season (nominal, wet and dry), and the interaction term. Each survey was treated as an independent sample in our analysis. We began with all factors in the model and then used the Wald statistic to perform backward stepwise elimination until only significant variables remained in the model (NORUŠIS/SPSS, 1999). Logistic regression uses maximum likelihood algorithms to estimate the probability of occurrence. However, when sample sizes are small or categorical predictor variables include one or more levels with no observations, maximum likelihood estimates are unreliable. This occurred when damselflies were uncommon (< 4 total detections) or were entirely absent from some sites (e.g., *Proischnura subfurcatum*). For three species (*Ceriagrion glabrum, Chlorocnemis marshalli superba, Africallagma pseudelongatum*), there were fewer than four detections throughout the study. Data for these species were not included in the analysis due to the small sample size. In these cases, we describe patterns of distribution qualitatively. For four other species (*Chlorocypha tenuis, C. trifaria, Proischnura subfurcatum*, and *Pseudagrion spernatum*) logistic regression was problematic, because these species occurred at some sites but were entirely absent from other sites. To facilitate model convergence we added a single observation to the sites in which those species were not detected. This simple adjustment allowed us to estimate differences among sites, and did not change estimates of seasonal effects. All statistical tests were conducted using SPSS (10.0), and results were considered statistically significant at $P < 0.05$.

LIMNOLOGICAL CHARACTERS

During the survey period, bi-monthly rainfall ranged between 1 mm and 253 mm. The mean monthly rainfall during the wet season (mean = 256) was greater than during the dry season (mean = 98). Limnological parameters also differed between seasons. In general, conductivity was higher during the dry season and lower in the wet season (Fig. 3). Dissolved oxygen also varied between seasons, but the magnitude of this variation differed among sites (Fig. 3). The most extreme variation in dissolved oxygen occurred at the Njuguta Swamp Stream, where wet season levels neared saturation and dry season levels dropped to 1.94 mg l^{-1} (Fig. 3). Water temperature and conductivity varied little between seasons. Within sites, there were few significant correlations among limnological characters. However, conductivity was negatively correlated with water temperature at the Rwembaita Swamp ($r = -0.57$, $p = 0.010$) and Inlet Stream East ($r = -0.64$, $p = 0.003$).

Some limnological characteristics also differed among the four study sites. Dissolved oxygen and pH differed among sites in both the wet (dissolved oxygen: $P < 0.001$; pH: $P = 0.006$) and dry seasons (dissolved oxygen: $P < 0.001$; pH: $P < 0.001$; Tab. I). Dissolved oxygen and pH were lowest in the Rwembaita Swamp and highest in Mikana Stream in both seasons (Scheffe, $P < 0.05$, Tab. I). Mikana Stream did not differ from Inlet Stream East or the Njuguta Swamp Stream in wet season dissolved oxygen levels. Conductivity and water temperature did not differ significantly among sites in either season (Tab. I). Across four sites, pH was positively correlated with dissolved oxygen ($r_s = 1.0$, $P < 0.01$).

SPECIES DISTRIBUTION

During the study period, we observed 10 species of adult damselflies belonging to four families (Tabs IIa,b). The damselfly assemblages were very similar with respect to richness and seasonal occurrence at Inlet Stream East and Njuguta Swamp Stream. Very few species were unique to any one site. The exceptions were *Chlorocypha trifaria*, which was only recorded at Mikana Stream, and *Proischnura subfurcatum*, which is a common inhabitant of the Rwembaita Swamp throughout the year. Below is a synopsis of distribution information for each species observed during the study.

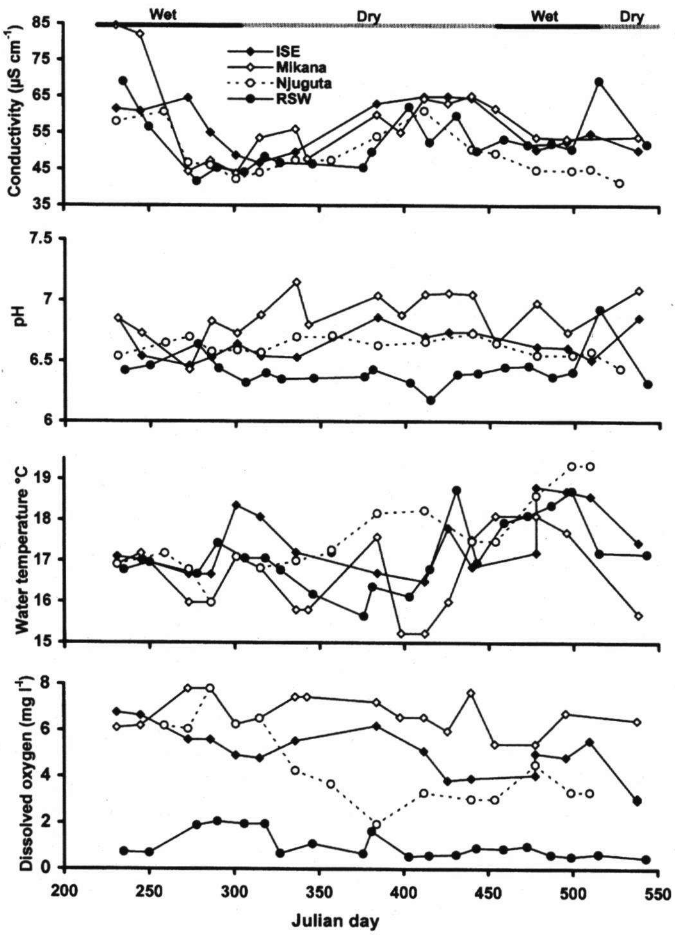

Fig. 3. Mean values of four limnological characters [conductivity (µS cm^{-1}), pH, water temperature (°C), and dissolved oxygen concentration (mg l^{-1})] measured throughout the study period (August 2000 to June 2001).

Table I

Mean values for limnological characters for four sites in a swamp-river system in Kibale National Park, Uganda. Differences among sites were detected using ANOVA with Scheffe contrasts (underlined sites are not significantly different). Sites are coded as follows: R = Rwembaita Swamp, N = Njuguta Swamp Stream, I = Inlet Stream East, and M = Mikana.

Character	Season	Mean	F	P	Scheffe contrasts
pH	Dry	6.67	63.58	< 0.001	R N I M
	Wet	6.61	4.94	0.006	R N I M
Conductivity	Dry	53.64	3.97	0.015	N R M I
(μS cm^{-1})	Wet	54.69	1.79	0.168	N R I M
Dissolved oxygen	Dry	4.08	76.13	< 0.001	R N I M
(mg l^{-1})	Wet	4.58	52.21	< 0.001	R I N M
Water temperature	Dry	16.93	3.79	0.18	M R I N
(°C)	Wet	17.54	0.401	0.754	M R N I

COENAGRIONIDAE

AFRICALLAGMA PSEUDELONGATUM (LONGFIELD). — There were not enough detections to statistically analyze predictors of occurrence. Males were only captured during surveys, but mating pairs were observed in tandem in July 2001 during non-survey times.

CERIAGRION GLABRUM (BURMEISTER). — Altogether we recorded three individuals during our study. In August of 2000 (n = 1) and 2001 (n = 2) pairs in tandem were seen in the interior of Rwembaita Swamp. In August 2001, a male was captured while it was eating an adult male *Proischnura subfurcatum*. There were not enough detections of this species to statistically analyze predictors of occurrence.

PROISCHNURA SUBFURCATUM (SELYS). — This was the only swamp specialist found within Kibale National Park. Logistic regression indicated site as a significant predictor for this species (Tab. III). This can be attributed to the absence of this species at all sites other than the swamp. Males were detected throughout the study period, and females were found during some of the dry (October, November, and June) and wet (August, October, April, and May) months. Copulation was observed only during the dry season (November, March, and June).

PSEUDAGRION HAGENI TROPICANUM PINHEY. — Logistic regression indicated that the probability of its occurrence varied among sites (Tab. III). Examination of parameter estimates indicated that when compared to Rwembaita Swamp the probability of occurrence was greater at Inlet Stream East and Njuguta Swamp Stream and less at Mikana Stream. In the Rwembaita Swamp this species was most common near channels of flowing water in the interior swamp. At the Njuguta Swamp Stream males were observed mate-guarding females during oviposition. Males continued to clasp females and completely submerged themselves below the surface of the water with the female during oviposition.

PSEUDAGRION KIBALENSE LONGFIELD. — Logistic regression indicated that the probability of its occurrence at Inlet Stream East and the Njuguta Swamp Stream was the same as Rwembaita Swamp, but greater at Mikana Stream (Tab. III). It was caught in tandem at Mikana Stream during both dry (December, January, and June) and wet (April) months, and also at Rwembaita Swamp in the wet season (April).

PSEUDAGRION SPERNATUM SELYS. — Logistic regression indicated no difference in the probability of detecting this species among the sites it occupied. However, its occurrence differed between seasons (Tab. III). Species detections were less probable during the wet season and greater during the dry season. It was captured in tandem only during the drier months of the year at the Njuguta Swamp Stream (December, February, and March) and in the Rwembaita Swamp (August and June).

CHLOROCYPHIDAE

CHLOROCYPHA TENUIS LONGFIELD. — Logistic regression indicate site as a significant predictor for the presence of this species (Tab. III). This may be attributed to the absence of this species at the Rwembaita Swamp. Examination of parameter estimates indicated that when compared to the Rwembaita Swamp, the probability of occurrence was greater at Inlet Stream East and Njuguta Swamp Stream, and less at Mikana Stream. Most captured individuals were males. A breeding pair was captured in tandem in the wet season (August) at Inlet Stream East. Otherwise, females were recorded at Inlet Stream East during wet (April and May) and dry (June) months and at Mikana Stream during a wet (May) month.

CHLOROCYPHA TRIFARIA (KARSCH). — Logistic regression indicated site as a significant predictor for this species (Tab. III). Males were observed in both wet and dry seasons, but only one female was captured throughout the study period.

PROTONURIDAE

CHLOROCNEMIS MARSHALLI SUPERBA SCHMIDT. — It inhabits small forest streams within the park, but is somewhat uncommon. We recorded only one adult male at the Mikana Stream. We expect that it occurs at low densities at other forest streams. *C. pauli* (Longfield), has been observed within the park, but was not observed during this study.

CALOPTERYGIDAE

UMMA SAPHIRINA FÖRSTER. — It was not included in the distribution analysis, although it was observed at both Mikana Stream and Inlet Stream East between May and August of 2000 and 2001. Data were not collected for this species during other months of the study period.

Table IIa

Seasonal presence of adult damselflies at Inlet Stream East and Mikana Stream from August 2000 to June 2001 – [M = ♂; – F = ♀; – B = ♂ and ♀; – T = pairs in tandem; – A_1, A_2, S_1, S_2, etc. refers to sampling periods 1 and 2 in the months indicated]

Inlet Stream East

	Season	Wet									Dry								Wet			Dry		
	Month	A_1	A_2	S_1	S_2	O_1	O_2	N_1	N_2	N_3	D_1	D_2	Ja_1	Ja_2	F_1	F_2	Mr_1	Mr_2	A_1	A_2	My_1	My_2	Jn_1	Jn_2
	Species																							
Coenagrionidae	*Africallagma pseudelongatum*				—						—	—												
	Ceriagrion glabrum				—						—	—												
	Proischnura subfurcatum				—						—	—												
	Pseudagrion hageni tropicanum	M	M	M	—	M	M	M	M	T	—	—	M	M	M	M	M	M	M		M	M	M	M
	Pseudagrion kibalense	M	M	M	—						—	—	M	M		M			M			M		
	Pseudagrion spernatum			M	—	M			M		—	—	M	M	M	M	M	M				M		M
Chlorocyphidae	*Chlorocypha tenuis*	T		M	—	M		M	M	M	—	—		M	M	M	M			B	M	B	B	B
	Chlorocypha trifaria				—						—	—												
Protoneuridae	*Chlorocnemis marshalli superba*				—						—	—												

Mikana Stream

	Season	Wet									Dry								Wet			Dry		
	Month	A_1	A_2	S_1	S_2	O_1	O_2	N_1	N_2	N_3	D_1	D_2	Ja_1	Ja_2	F_1	F_2	Mr_1	Mr_2	A_1	A_2	My_1	My_2	Jn_1	Jn_2
	Species																							
Coenagrionidae	*Africallagma pseudelongatum*		—	—	—						M	—												—
	Ceriagrion glabrum		—	—	—							—												—
	Proischnura subfurcatum		—	—	—							—												—
	Pseudagrion hageni tropicanum		—	—	—		M					—			M									—
	Pseudagrion kibalense		—	—	—	M	M	M	M	M	T	—	M	T	M	M	M	M	M	T	M	M	T	—
	Pseudagrion spernatum		—	—	—							—												—
Chlorocyphidae	*Chlorocypha tenuis*		—	—	—				M		M	—				M				M	B	M	M	—
	Chlorocypha trifaria	M	—	—	—							—	M			M				B		M	M	—
Protoneuridae	*Chlorocnemis marshalli superba*		—	—	—							—								M				—

DISCUSSION

This study provides some of the first information on habitat associations and seasonal variation in occurrence of an Afrotropical damselfly community in East Africa. In Kibale National Park, limnological characteristics vary among sites and to a lesser degree between seasons. Our data suggest that inter-site variation in limnological features influences damselfly distribution. Two species appear to be habitat specialists, being associated exclusively with swamps that are characterized by extreme aquatic hypoxia. One species was found at the swamp and at two sites where the oxygen was not chronically low. Four species occupied at least at one of the sites characterized by moderate to high dissolved oxygen, but were not found in the hypoxic swamp. Two species were widespread and occurred in all habitat types surveyed. Many of these species were present throughout most of the year, with few examples of strong seasonal patterns of occurrence being detected.

INTERSITE VARIATION

Of the four limnological characters considered in this study, dissolved oxygen concentration was the most variable among sites. Although there was a positive correlation between average pH and dissolved oxygen among the four sites, the magnitude of fluctuation for these characters differed. Over the course of the study average pH ranged between 6.42 and 6.87 among the four sites. This represents a 7% difference among the sites. If pH is translated to hydrogen ion concentration, $[H^+]$, the range among sites was 1.4×10^{-7} to 3.8×10^{-7} M H^+, representing a 270% difference. Dissolved oxygen showed even greater variation among sites ranging between 1.01 and 6.71 mg l^{-1}, representing a difference of 664%.

The wide range in dissolved oxygen availability in this swamp-river system may be an important factor for damselfly distribution, though certainly other limnological features may also contribute to the patterns observed. Zygoptera, and more generally, tracheal gill breathers, tend to be more sensitive to hypoxia than other aquatic insect larvae such as atmospheric breathers (e.g., Nepidae, Dytiscidae, and Hydrophilidae as larvae and adults) and transportable air store breathers [e.g., Dytiscidae (adult), Gyrinidae (adult), Naucoridae (larvae and adults)]. Tracheal-gill-breathing insects are more sensitive to low oxygen conditions, because they are benthic (MERRITT & CUMMINS, 1996) and extract dissolved oxygen from the aqueous environment by simple diffusion (WIGGLESWORTH, 1972). The occurrence of six damselfly species in the Rwembaita Swamp site, some of which occurred throughout the year, suggests a broad habitat representation in the Zygoptera and far-reaching adaptations to hypoxia in some zygopteran larval species.

For four of the nine species reported in this study, site was a significant predictor of occurrence. *Proischnura subfurcatum* and *Ceragrion glabrum* were the only species observed exclusively in the Rwembaita Swamp. The adult damselfly community assem-

Table IIb

Seasonal presence of adult damselflies at Njuguta Swamp Stream and Rwembaita Swamp from August 2000 to June 2001 – [M = ♂; – F = ♀; – B = ♂ and ♀; – T = pairs in tandem; – A_1, A_2, S_1, S_2, etc. refers to sampling periods 1 and 2 in the months indicated]

Njuguta Swamp Stream

	Season					Wet								Dry						Wet				Dry
	Month	A_1	A_2	S_1	S_2	O_1	O_2	N_1	N_2	N_3	D_1	D_2	Ja_1	Ja_2	F_1	F_2	Mr_1	Mr_2	A_1	A_2	My_1	My_2	Jn_1	Jn_2
Family	Species																							
Coenagrionidae	*Africallagma pseudelongatum*		—						—					—		—				—				—
	Ceriagrion glabrum		—						—					—		—				—				—
	Proischnura subfurcatum		—						—					—	M	—				—				—
	Pseudagrion hageni tropicanum	M	—	M	M	M	M	M	—	M	M		M	—	M	—	M	M	M	—	M	M	M	—
	Pseudagrion kibalense		—			M			—					—		—	M			—				—
	Pseudagrion spernatum		—		M			M	—	M		T	M	—	T	—	M	T	M	—	M	M		—
Chlorocyphidae	*Chlorocypha tenuis*		—		M				—		M		M	—	M	—	M	M	M	—	M	M		—
	Chlorocypha trifaria		—						—					—		—				—				—
Protoneuridae	*Chlorocnemis marshalli superba*		—						—					—		—				—				—

Rwembaita Swamp

	Season					Wet								Dry						Wet				Dry
	Month	A_1	A_2	S_1	S_2	O_1	O_2	N_1	N_2	N_3	D_1	D_2	Ja_1	Ja_2	F_1	F_2	Mr_1	Mr_2	A_1	A_2	My_1	My_2	Jn_1	Jn_2
Family	Species																							
Coenagrionidae	*Africallagma pseudelongatum*		—		—							—							M				M	—
	Ceriagrion glabrum		—		—							—										F	T	—
	Proischnura subfurcatum	B	—	M	—	B	B	M	T	M	M	—	M	M	M	M	T	B	M	B	B	M	T	—
	Pseudagrion hageni tropicanum		—		—				M	M	M	—	M	M	M	M	M	M		M	M			—
	Pseudagrion kibalense		—		—							—								T	M	M		—
	Pseudagrion spernatum	T	—		—		M	M	M		M	—	M	M	M		M				M		T	—
Chlorocyphidae	*Chlorocypha tenuis*		—		—							—												—
	Chlorocypha trifaria		—		—							—												—
Protoneuridae	*Chlorocnemis marshalli superba*		—		—							—												—

blage within the Rwembaita Swamp is segregated between areas of stagnant and flowing water. *Proischnura subfurcatum* and *Africallagma pseudelongatum* were generally found near standing pools of stagnant water, while the other species observed in the swamp, *Pseudagrion hageni tropicanum*, *P. kibalense*, and *P. spernatum*, were mainly found in or near channels of flowing water (C. Apodaca, pers. observ.). The latter species were also observed at stream sites where mean dissolved oxygen levels were moderately high (5.0 mg l^{-1} for Inlet Stream East and 4.3 mg l^{-1} for Njuguta Swamp Stream), but they were seasonally rare (*P. hageni tropicanum*) or absent (*P. spernatum*) from Mikana Stream, a site characterized by faster current and higher dissolved oxygen levels (mean dissolved oxygen concentration = 6.7 mg l^{-1}). Both chlorocyphid species, *Chlorocypha tenuis* and *Chlorocypha trifaria* were only found at stream sites, and *C. trifaria* was restricted to Mikana Stream along with the protoneurid *Chlorocnemis marshalli superba*. The other members of the damselfly community were recorded at all four sites.

In Uganda, and East Africa in general, few zygopteran larvae have been linked to adult forms; however, the distribution and behavior of the adults may correlate with patterns of larval distribution. In Kibale National Park, some zygopteran larvae that have been recorded at various aquatic sites tend to support patterns of adult distribution. For example, in the Rwembaita Swamp, *P. subfurcatum* is the dominant larval zygopteran and has not been observed in stream or river sites in the park (APODACA, 2003). The low dissolved oxygen levels that we observed in the Rwembaita Swamp are not unusually low for papyrus swamps or other heavily vegetated swamps in the region (BEADLE, 1932; CARTER, 1955; CHAPMAN et al., 1998, 2000, 2001). Based on distribution patterns of temperate zygopterns, this would represent stressful conditions for many temperate species (LAWTON, 1971; ERIKSEN, 1986). However, given the widespread nature of hypoxia in tropical fresh waters, it is possible that many aquatic insect groups have evolved to exploit such habitats. For example, some zygopteran larvae occupy the oxygen-scarce waters found in tree holes in tropical regions (DE LA ROSA & RAMIREZ, 1995). Thus, the ability to physiologically and/or behaviorally deal with low oxygen conditions may be pronounced in a suite of tropical damselfly larvae.

SEASONAL PATTERNS OF OCCURRENCE

Early investigators (KUMAR, 1976; CORBET, 1964; GAMBLES, 1960) suggested that rainfall patterns are extremely important in determining the seasonal distribution of some odonates in highly seasonal tropical areas. In general, our results suggest that seasonal fluctuations in rainfall have little effect on the flying season of adult damselflies in Kibale National Park. *Pseudagrion spernatum* was the only species with a flight season that correlated with rainfall pattern. It was more likely to be observed in the dry season and was found across several months in both swamp sites. Thus, its probability of occurrence was highest was dissolved oxygen was low. If adult activity reflects larval distribution, we anticipate high tolerance to hypoxia in the larvae of this species. Both *Ceragrion glabrum* and *Africallagma pseudelongatum* were most active in the dry season and also found in the Rwembaita Swamp. However, our small sample size for these species and for *Chlorocnemis marshalli superba* did not allow us to statistically test for significant predictors of occurrence. PARR (1984) found seven categories of flight activity for odonates in Liwonde National Park, Malawi. With a greater sample size, our data for some species may fit a similar pattern; however, in general, season was not a significant predictor of occurrence.

In areas where rainfall is more evenly distributed throughout the year, organisms may show a less pronounced response to seasonal change. Among tropical regions, there is great variation in the onset, duration, and magnitude of the wet season. At high latitudes, dry seasons may be severe and long, and produce strong seasonal variation in the availability and quality of aquatic habitats (e.g., northern Costa Rica, CHAPMAN & KRAMER, 1991), whereas in some equatorial regions, biannual rains or more continuous rainfall can buffer strong seasonal effects (e.g., central Congo basin, CHAPMAN & CHAPMAN, 2003). KUMAR (1976) reported a single annual rainfall peak of about 450 to 580 mm between August and mid-September in the Dumar Valley of India, where he investigated seasonal regulation of Zygoptera lifecycles. In this region, most adult activity, including breeding, takes place either before or after the wet season. In contrast, many damselflies in Kibale National Park are active throughout the year. This may reflect the pattern of biannual rainfall that creates more even dispersion of rainfall throughout the year. Clearly, there are seasonal cycles in limnological characters (e.g., dissolved oxygen at the swamp sites, this study and CHAPMAN et al., 1998, 2000), but they are not as pronounced as in some other tropical regions; and this may produce more seasonally consistent habitat availability for the zygopteran fauna.

Our data suggest unregulated (not limited by season or habitat availability, essentially year-round) larval development in some species in Kibale National Park. Examples of unregulated development are most common in coenagrionids in lowland tropical areas (CORBET, 1999). The year round presence of adult *Proischnura subfurcatum* and *Psuedagrion hageni* suggest that these species, like other members of their family, may follow an unregulated emergence pattern. However, until we know more about emigration and the duration of the adult and larval periods for these species, it will be difficult to understand regulatory patterns governing their development. Lab-rearing experiments also will be required to fully understand emergence patterns, since the larval population is represented by several overlapping age classes (CORBET, 1999).

CONSTRAINTS OF THE SAMPLING PROTOCOL

The number of species observed during our surveys did not include all those known to occur in Kibale National Park. Two previously reported species, *Pseudagrion kersteni* and *Chlorocnemis pauli* (DIJKSTRA & DINGEMANSE, 2000), were not detected in our study. This may indicate that our survey method was not fully effective in detecting the seasonal presence of less common species, or that these species are extremely rare with periodic, perhaps supra-annual occupation of the habitats.

When surveying for adult Zygoptera it is important to take their thermal range of activity into account, since ambient temperature can affect activity patterns of adult odonates (MAY, 1977). Even if a species is present, it may not be active during all times of the day (LUTZ & PITTMAN, 1970). We tried to survey during the warmest times of the day, however, surveying in the rain was sometimes unavoidable. Thus, not all surveys were conducted under optimal environmental conditions for adult activity.

Most individuals captured during our surveys were males. These results are consistent with previous reports of odonate males outnumbering females at water (CORBET, 1999; CORBET, 1962; JOHNSON, 1963; WAAGE, 1980), but this large discrepancy probably does not reflect the actual sex ratio of the adult population. It is more likely an artifact of the sampling protocol. Male behavior is more conspicuous, and surveys conducted at the waterside tend to detect a greater proportion of males than females (MICHIELS & DHONDT, 1989). In fact, some investigators (BICK & BICK, 1968) have reported male biased sex ratios of up to 75% in damselfly populations. This is in part due to differences in activity schedules and habitat preferences between the sexes. Females visit the waterside as they become ready to breed, and males generally compete for territories near water where they wait for receptive females. Additionally, males and females of some species are active during different times of the day (MICHIELS & DHONDT, 1989). Therefore, searching only at water can bias interpretations of flight activity, but should be sufficient to detect which species occupy a site.

ACKNOWLEDGEMENTS

Funding for this research was provided by the Wildlife Conservation Society, Sigma Xi, The Center for African Studies (University of Florida), and the Ford Foundation. We thank JAMES MAGARO, JOVAN MUGENYI, and MARGARET KEMIGISA of the Kibale Fish and Monkey Project for their participation in field collections. We thank VIOLA CLAUSNITZER for use of her unpublished key to East African odonates and K.-D.B. DIJKSTRA for assistance with identifying damselfly specimens. Permission to conduct research in Uganda was acquired from the National Council for Science and Technology and the Makerere University Biological Field Station of Uganda. We also thank FRANK NORDLIE, JAMES NATION, DAVID JULIAN, and NAT SEAVY for comments on an earlier version of this manuscript.

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