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SITE FIDELITY AND DISPERSAL OF ADULT *NEUROBASIS AWAMENA* MICHALSKI IN TROPICAL RAINFOREST STREAMS IN PAPUA NEW GUINEA (ZYGOPTERA: CALOPTERYGIDAE)

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The sp. inhabits swift mountain streams at montane elevations of southern Papua New Guinea. In this study the duration for which adult ♂♂ and ♀♀ remained at a given site in rainforest streams was determined, and the dispersal distance and direction of marked individuals leaving the site of initial observation was assessed. Territorial defence was non-exclusive and ♂♂ held territories for up to 45 days. On average, ♂♂ remained 9 days, ♀♀ 11 days at a given site. Both sexes stayed significantly longer at sites with suitable oviposition substrates than at a site without. Mating occurred only twice during the study period, and the scarcity of mating events might explain long territory holding times. On a daily basis ♂♂ moved larger distances than ♀♀, suggesting that ♀♀ remain at a site for a longer period before moving a long distance. Both sexes showed similar lifetime dispersal distances (1000-1300m), and dispersal was predominantly directed upstream. It is concluded that this unidirectional dispersal of adults may compensate for downstream drift of larvae in rapid flowing streams.

INTRODUCTION

Many species of demoiselle damselflies (Zygoptera: Calopterygidae) are known to exhibit territorial behaviour along water courses suitable for reproduction (CORBET, 1999; SILSBY, 2001). Territories are established by males at sites that have attractive oviposition features for females (MARDEN & WAAGE, 1990; PLAISTOW & SIVA-JOTHY, 1996; GONZÁLES-SORIANO & CÓRDOBA-AQUILAR, 2003), and duration of territory holding might have consequences for lifetime reproductive success (KEMP & ALCOCK, 2003). While many studies have determined the behavioural aspects and evolutionary benefits of territoriality, the temporal aspect of site fidelity has rarely been addressed (CLAUSNITZER, 1996; BEUKEMA, 2002b).

The tropical calopterygid *Neurobasis awamena* is a recently discovered species of mountain streams in montane elevations along the southern scarp of the central mountain range of Papua New Guinea (J.C. Michalski, pers. comm.). The genus *Neurobasis* generally inhabits swift and rocky mountain streams, and males are known to establish territories by embarking on aerial display fights (LIEFTINCK, 1955). Females oviposit into the rootlets of trees well below the water surface, and adult *Neurobasis* are assumed to remain close to the place of their emergence (LIEFTINCK, 1955).

In this study the length of time that adult *N. awamena* remain at a given stretch of mountain stream was examined, in order to determine whether males remain at a site longer than females. Site fidelity for both sexes was also compared between locations with and without suitable oviposition substrates. Furthermore, the distances travelled by colour-marked individuals were investigated, in order to test whether there are differences between males and females in dispersal distances (CONRAD et al., 1999, 2002), and in the direction of dispersal. Dispersal direction has been hypothesized to be random for some damselfly species (MOORE, 1954; CONRAD et al., 2002), but appears to be directional in some rheophilic species (BEUKEMA, 2002a). In this study it was also examined whether adult *Neurobasis awamena* show a distinct preference for upstream or downstream dispersal.

METHODS

STUDY AREA – The study was carried out between February and June 2004 at Crater Mountain Biological Research Station (CMBRS), in the southern scarp of the central mountain range of Papua New Guinea (06°43'S; 145°05'E; 900m a.s.l.). The site lies within a large continuous tract of pristine, aseasonal, lower montane rainforest, and features a large number of clear rocky mountain streams. The terrain is very rugged and creek drainages are usually separated by steep, forested ridgelines. Two larger rivers run through the study area, and are fed by numerous smaller tributaries, which form the main habitat for Neurobasis awamena. Due to the rugged terrain the tributaries are generally less than 2000 m long.

FIELD MEASUREMENTS – From February through June 2004 I caught and marked mature adult *N. awamena* in easily accessible creeks in the centre of the study area. The damselflies were caught with a nylon net and marked with either liquid paper correction fluid or white permanent marker pen on the underside of the hindwings (THOMPSON, 2000; WATANABE & MIMURA, 2003). Each individual was given a unique combination of coloured symbols that was readily recognizable without recapturing the individual. Damselflies were released immediately after marking at the same spot where they were caught. This site was then checked on a daily basis for the following weeks, and the position of every marked individual was recorded. Movements of up to 15m from the marking spot were not considered as dispersal, as they were mostly associated with small-scale displacement in search of sunlit areas, and individuals returned to the marking spot afterwards. If individuals were not found at their previous location, a 100-300m section of the stream was searched. Upon resighting a marked individual, distance and direction (upstream or downstream) from the point of capture were recorded with a tape measure, following an assumed flight path along the creek. Once every two weeks several, arbitrarily chosen creeks in which no *N. awamena* had been marked were also searched for dispersed individuals. If individuals were found in another drainage, the dispersal distance was measured along the waterways, not in a straight line between creeks.

For every marked individual the number of days it remained at a specific location (site fidelity), the survival time, and the maximum (or lifetime) dispersal distance were obtained. Both survival and dispersal figures have to be regarded as minima. Firstly, because individuals might have moved further but evaded detection, and secondly, because survival and dispersal prior to capture and marking remain unknown. The habitat at the marking site was classified as either suitable or unsuitable for reproduction. This was assessed by the respective presence or absence of small, submerged rootlets along the banks of the creek, which are used by female *N. awamena* as oviposition substrate (LIEFTINCK, 1955; pers. obs.).

ANALYSIS – The site fidelity and dispersal distances of males and females were compared using non-parametric Mann-Whitney *U*-tests. Dispersal distances were analysed both on an individual basis (maximum dispersal distance) and on the basis of the daily records. Upstream and downstream dispersal distances were compared for males and females, in order to test for differences in dispersal direction. The survival times of males and females were compared using analysis of variance (ANOVA). Regression analysis was used to test whether distance from the point of marking increased with time. This was done for both sexes combined, as well as separately for males and females. All results are given as mean ± SD. Statistical analyses were carried out using SPSS software (NORUSIS, 2000).

RESULTS

A total of 66 adult *Neurobasis awamena*, 44 males and 22 females, was marked. Males remained at their site of capture for an average of 8.7 days, females remained at the site for an average of 10.6 days (Tab. I). Due to the high variability in site fidelity times the difference between males and females was not significant. There were proportionately slightly more females staying for extended periods than males (Fig. 1), and proportionally more females staying within 20 m of their marking location than dispersing further than 20 m (Fig. 2). One male remained 45 days at the capture site, females remained up to 36 days at the capture site (Tab. I). Both sexes survived 12-13 days on average, and there was no significant difference in survival time ($F = 1.573$; $p = 0.217$). However, the recorded maximum for males was almost twice as high as for females (Tab. I)

The length of stream utilized by males around a site was generally slightly larger (ca 15 m) than that utilized by females (ca 7 m). Territory holders sometimes initiated agonistic display flights with con-specifics, but this was not

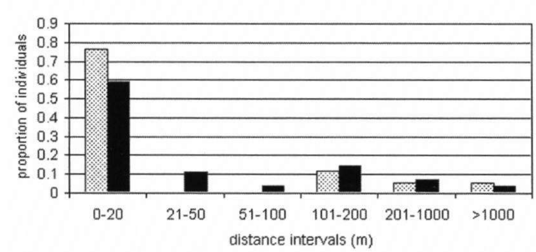

Fig. 1. Relative proportions of site fidelity time of *Neurobasis awamena* males (black, n = 44) and females (stippled, n = 22) in mountain creeks at Crater Mountain Biological Research Station, Papua New Guinea.

Table I
Site fidelity, survival time, and maximum and daily dispersal distances for male and female *Neurobasis awamena* in creeks at Crater Mountain Biological Research Station, Papua New Guinea

	Males (n = 44)		Females (n = 22)	
	mean ± SD	max	mean ± SD	max
site fidelity (days)	8.7 ± 11.4	45	10.6 ± 11.7	36
survival (days)	12.6 ± 17.0	61	12.8 ± 11.9	36
maximum dispersal distance (m)	99.3 ± 209.6	1010.0	123.4 ± 319.4	1300.0
daily dispersal distance (m)	51.4 ± 154.1	355.0	16.4 ± 116.7	200.0

a general rule and unpredictable. Territory defence was most pronounced between 9:30 and 13:00 hrs, but even during this time territories were not defended exclusively. Some males would perch only 50 cm apart without any obvious sign of aggression. Similarly, mate guarding was not very pronounced. In one instance three adult males passed through the territory of a pair that had just separated after copulation. Even though the intruding males hovered and circled around the female they were not harassed by the territorial male with which she had mated. The territorial male remained within 3 m during the time the female was ovipositing, but made no attempt to chase away intruders. Only two copulation and oviposition events were observed throughout the study period.

Females were not recorded to disperse after having been stationary for 7 days at a site. In males however, dispersal was observed even after individuals had been sedentary for a long time (> 12 days). One individual left after 45 days at one site, and was recorded 10 days later in a different drainage, 1010m from its capture locality. The rate of resighting after dispersal was 18% for females and 20% for males. The maximum lifetime dispersal distance recorded for a female was 1300m upstream along one of the main rivers of the study area. Dispersing females had travelled at least 196 m from their site of capture before being resighted. Even though there was no significant difference between maximum dispersal distances in males and females, proportionally more males dispersed > 50 m from their capture location than females (Fig. 2). The daily dispersal rates were significantly higher for males than for females (z = -9.42, p < 0.001; Tab. I).

There was no correlation between time and dispersal distance in either males or females, and dispersal occurred mostly in discrete events.

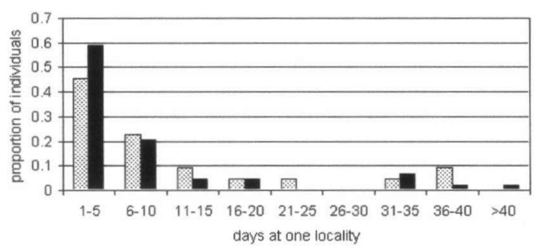

Fig. 2. Relative proportions of total dispersal distance by *Neurobasis awamena* males (black, n = 27) and females (stippled, n = 17), measured from their capture location in mountain creeks at Crater Mountain Biological Research Station, Papua New Guinea.

Net-dispersal was generally directed upstream. Both for males and females the upstream dispersal distances were significantly higher than the downstream dispersal distances ($z = -9.72, p < 0.001$ for males; $z = -6.58, p < 0.001$ for females). The maximum downstream dispersal distance was 200 m for males and 15 m for females, whereas maximum upstream dispersal was 1010 m and 1300 m, respectively.

One of the marking locations differed from all other locations in having a lower gradient and slower water flow rate. There were no submerged rootlets present along the banks of this creek. Individuals marked at this site stayed on average only 2.9 ± 2.5 days ($n = 27$, maximum = 10 days), as opposed to 13.9 ± 13.0 days ($n = 39$) in locations with suitable oviposition sites ($z = -4.62, p < 0.001$). Most individuals marked at the former location had disappeared from the site by the following day. Despite the short residency time of individual damselflies at this location, an approximately equal number of adult and subadult damselflies could be recorded there every day throughout the study period. There was a high proportion of teneral males among the damselflies observed at this locality, but the actual ratio was not quantified.

DISCUSSION

In the study area near Crater Mountain, female *Neurobasis awamena* remained on a given stretch of stream slightly longer on average than did males, and a larger proportion of females than males stayed for extended periods. Even though these differences were not significant, the results do indicate that females do not move around extensively as has been found in other calopterygid studies (THOMPSON, 2000), but rather stay close to a site that may offer good oviposition opportunities.

The differences in territorial male residency time might reflect differences in territory quality (HILFERT-RÜPPELL, 1999). Better quality territories would require more effort to defend and could therefore only be held for shorter times (SWITZER, 2002). It is therefore likely that the males holding territories for more than 35 days occupied suboptimal habitat with very little competition. To test these hypotheses further investigations are required in which habitat quality is critically assessed.

Territoriality was non-exclusive. From the observations in this study it was not apparent when or what territories were defended, and when and where conspecific males were tolerated. As noted in other studies, territorial behaviour was most prominent between 9:00 and 13:00 local time (HAMILTON & MONTGOMERIE, 1989; CLAUSNITZER, 1997; HILFERT-RÜPPELL, 1999; DE MARCO & RESENDE, 2002; DE MARCO & CARDOSO PEIXOTO, 2004). Even during this time some intruders were not attacked. A possible explanation might be the advantage of resident males over intruders, deterring newcomers from challenging the territory holder (SWITZER, 2004). A lack of aggression was even noted between a guarding male and other males harassing an ovipositing female. Sperm removal by rival males has been found in several damselfly species (FINCKE, 1984; WAAGE, 1986; LINDEBOOM, 1998; GONZÁLES-SORIANO & CÓRDOBA-AGUILAR, 2003), and constitutes a major cost to reproductive success, usually prevented by mate guarding (ALCOCK, 1982). However, mate guarding has sometimes been observed to be almost absent in other *Neurobasis* species (KUMAR & PRASAD, 1977; GUNTHER, 2002). The absence of close mate-guarding after copulation has been hypothesised to result from the elaborate display required prior to mating in some calopterygids, rendering a take-over unlikely during the short time span between copulation and oviposition (KUMAR & PRASAD, 1977; THOMPSON, 2000). A further explanation for *N. awamena* could be the submerged oviposition behaviour of the female (LIEFTINCK, 1955), which would make it inaccessible to competing males during oviposition.

The site fidelity times of *N. awamena* are considerably larger than those of other calopterygids (THOMPSON, 2000; SILSBY, 2001; BEUKEMA, 2002b; NARAOKA, 2003), and equal or exceed those of larger dragonflies (CLAUSNITZER, 1996). The long territory occupation might be required by the relative scarcity of mating events. Only two copulations were observed during the four month study period, which is consistent with the infrequent mating observed in some other calopterygids (LIEFTINCK, 1955; ALCOCK, 1982; THOMPSON, 2000). The extended period of territoriality might limit the energy available for defensive behaviour, thus providing a potential explanation for the non-exclusive territoriality as a measure to preserve energetic resources. Tolerating conspecific intruders for a short time, but in return being able to hold the territory for a longer time, might increase lifetime reproductive success (PLAISTOW & SIVA-JOTHY, 1996; KEMP & ALCOCK, 2003).

Site fidelity was more pronounced in areas suitable for reproduction. From this it can be assumed that both males and females recognized high quality sites, as has been demonstrated for other calopterygids (HILFERT-RÜPPELL, 1999). Since more females are attracted to sites with better oviposition opportunities (ALCOCK, 1987; WAAGE, 1987), males can be expected to increase their mating chances by occupying these sites for a longer time.

Despite the short residency times at the low quality site, the number of adult and subadult *N. awamena* was fairly constant between days. This suggests that dispersing adults appeared at this site in passage, and highlights the continuous movement of a substantial part of the population (EBERHARD, 1986). Even though data on the ratio of teneral vs. adult males at this site are anecdotal, the observation of several teneral males in this site as opposed to no other site might indicate that teneral individuals do not remain at their emergence site but disperse widely. This and the dispersal distances recorded for adults disprove LIEF-

TINCK's (1955) assumption that *Neurobasis* damselflies remain close to their emergence site.

Most of the dispersing damselflies, which were all mature adults in this study, moved upstream. This might be an adaptation to compensate for downstream drift of the larvae (BEUKEMA, 2002a). Given the generally rapid water speed of the inhabited creeks, and the long larval development of calopterygids (CORBET, 1999), downstream drift of larvae seems highly likely (BRITTAIN & EIKELAND, 1988). Larvae might accumulate at sites with slower water speed, thus potentially explaining the high proportion of teneral individuals observed at the site without oviposition substrate.

Dispersal occurred mostly in discrete events, and time was an insufficient predictor for distance from the capture location in both males and females. Males displayed a much higher daily dispersal rate than females, suggesting that dispersal in males is more stepwise than in females, as has been noted in other studies (EBERHARD, 1986; HILFERT-RÜPPELL, 1999; BEUKEMA, 2002a). Females had slightly higher lifetime dispersal distances than males, which is consistent with findings for other damselflies (CONRAD et al., 2002; ANGELIBERT & GIANI, 2003). No females were recorded at distances between 15-195 m away from their capture locations. This suggests that females tend to stay longer in one place before moving a large distance to a new location, whereas males stay shorter times at several locations that may only be 40 m apart. This behaviour might be explained by the attempt to maximize mating success in males that did not mate for a given period of time and thus decide to move on (HILFERT-RÜPPELL, 1999; SWITZER, 2002).

Calopterygid damselflies are known as good dispersers, with individuals of several species having been recorded to travel more than 1 km (STETTMER, 1996; THOMPSON, 2000; BEUKEMA, 2002a, 2002b; PARR, 2004). The maximum dispersal distance found in this study is therefore comparable to other members of the family, and significantly higher than for some pond damselflies (CONRAD et al., 2002).

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