Male rarity and putative sex-role reversal in Fijian damselflies (Odonata)

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Abstract: Behavioural sex-role reversal occurs when males and females exchange their standard roles in territorial defence or parental care. One circumstance under which sex-role reversal may occur is when males are a limiting resource, so that females have to compete for access to mates. Here we report on male rarity and male and female behaviour of species within the damselfly genus *Nesobasis*, endemic to Fiji. Earlier reports suggested that, in some members of this genus, males were seldom observed and that females of these species were consequentially territorial, a phenomenon described as 'sex-role reversal'. Quantitative estimation of the ratio of adult males to females at 15 localities in 13 *Nesobasis* species (1489 individuals) indicated that males were extremely rare in some species, yet common in others. This interspecific variability in male rarity cannot be explained by elevation or habitat. Formal observations of three species with abundant males revealed that males of these species were highly territorial: they physically challenged intruders while remaining within a confined area. By contrast, in three species where males were consistently rare or absent, females were not territorial: instead, they moved widely and were primarily engaged in oviposition. While we do not know the underlying reason for the unusual rarity of males at oviposition sites in some species, it is clear that this rarity has not provided sufficient selection pressure to generate genuine sex-role reversal.

Key Words: Fiji, insects, male rarity, mating system, Odonata, Pacific, sex-role reversal, territoriality

INTRODUCTION

Sex-role reversal, with females competing for males that are choosy, is expected to occur where there is high male parental investment (Bonduriansky 2001, Emlen & Wrege 2004, Gwynne & Simmons 1990, Svensson & Petersson 1988, Wilson *et al.* 2003). Sex-role reversal in species not showing parental care has also been observed, but there are fewer examples. In some populations of the butterfly *Acraea encedon* for instance, males are a limiting resource (Jiggins *et al.* 2000). In these cases, female behaviour changes dramatically, with females swarming at landmarks to attract the occasional male.

Here we report on another alleged case of sex-role reversal, this time in damselflies (Zygoptera: Odonata). Damselflies do not provide parental care and they are obligate aquatic organisms, in that their immature (larval) stage is spent in freshwater habitats (Corbet 1999). Their life cycle consequently requires that adult females return to the water to lay eggs. Typically, mating also takes place at the water, and males commonly aggregate at the water to intercept females. Male competition for gravid females often results in male territorial behaviour (Conrad & Pritchard 1992, Corbet 1999), either as a means of monopolizing oviposition sites, or to defend good vantage points for the detection of females (Grether 1996, Switzer & Eason 2003). While males aggregate at the water, females will typically forage away from water undisturbed by mate-searching conspecific males: as a consequence, adult males generally outnumber females at the site of reproduction (Corbet 1999).

In this paper we have quantified the relative rarity of adult males at the site of oviposition and examined

both male and female adult behaviour in a number of members of the damselfly genus *Nesobasis* (Zygoptera: Coenagrionidae), which is endemic to Fiji. *Nesobasis* ranks among one of the most species-rich genera of Odonata found in any oceanic island group in the world (Donnelly 1990). In several species of this extraordinary genus, males have previously been reported to compete for females and to show territorial behaviour (Donnelly 1990). Intriguingly, it has been suggested that in other *Nesobasis* species it is the females rather than the males that compete for access to mates, actively establishing and defending territories (Corbet 1999, Donnelly 1990, 1994; Silsby 2001). In these putative 'role-reversed' species, conspecific males were rare or absent at the site of oviposition, and it has been suggested (Donnelly 1990) that the territorial behaviour in females might have arisen as a consequence of this rarity of the opposite sex. This proposal is not without justification: both male rareness at the site of reproduction and female territorial behaviour are extremely unusual in odonates (Corbet 1999). Moreover, experimental work has shown that the removal of males in a natural population of *Perithemis tenera* (Odonata: Anisoptera) caused females to manifest territorial behaviour (Jacobs 1955).

Our research had two main aims. First, we set out to quantitatively test whether males were rare at the site of oviposition in some species of *Nesobasis*, but not in others. In relation to male rarity we investigated whether environmental differences between sites could help explain patterns. Second, we wished to test whether relative male rarity had any influence on male and/or female behaviour (or vice versa). If members of this damselfly genus were territorial, we predicted that males at male-biased sites would aggressively defend small sections of streams from other individuals, while conspecific females would not (Corbet 1999). Likewise, we expected from prior remarks (Donnelly 1990) that females at sites where males are rare would exhibit territorial behaviour, while conspecific males would not.

METHODS

Members of the genus *Nesobasis* occur in all stream habitats on the Fijian Islands, excluding large rivers (Donnelly 1990). We sampled populations on the two biggest islands: Viti Levu (17°S; 177°E) and Vanua Levu (16°S; 179°E). We also sampled on two smaller islands: Ovalau (18°S; 179°E) and Kadavu (19°S; 178°E). Different islands within Fiji contain different species of *Nesobasis*, so the sampling of multiple islands allowed us to examine a larger number of species (Beatty *et al.* 2007, Donnelly 1990). In August and September of 2005 we mainly sampled sites on Viti Levu, but we were also able to

include some sites on Vanua Levu. In August and September of 2006 we sampled further sites on Vanua Levu and also sampled on the islands of Kadavu and Ovalau. While our surveys were restricted to the dry season over two separate years, Donnelly made a total of seven visits to Fiji at different times of year, and always had the same impression that in some species males were rare and the females of the species were territorial (pers. comm.). Moreover, a separate expedition by one of the co-authors (JHS) in January and February 2006, likewise found very few males of *N. rufostigma*, yet an abundance of females.

Male rarity

To estimate ratios of males to females at the site of oviposition we visited suitable streams where we collected damselflies while slowly walking along the stream, netting all individuals observed at the water or at the streamline (up to 2 m from the stream). We then identified and sexed each individual. As is typical for damselflies, males in *Nesobasis* species are similar to (or somewhat more conspicuous than) females in phenotype and behaviour. Therefore if any subtle sampling bias exists, we feel that the number of females may be (at worst) marginally underestimated in our samples based on human detection.

In total we quantified male rarity in 13 species of *Nesobasis* for which our data complied with our selection criteria (see below). Whenever feasible, we sampled multiple sites per species. This allowed us to examine variation in male rarity at oviposition sites both within and among species. Not all species that we here include have been formally described, which explains our use of a combination of species names and coding to refer to species (see Beatty *et al.* 2007 for more details). For instance, we here include data on a species that is new to science, which we refer to as Uds 2. It is relevant to note that ongoing molecular and phylogenetic work (unpubl. data) confirm the species status of all species here included.

Whenever possible (i.e. where vegetation permitted) we also searched for damselflies up to 50 m from the water in shrubs and lower branches of trees. Using binoculars we also scanned higher branches of trees. The rationale for this additional sampling was to evaluate whether high concentrations of males reside away from the water. However, very few individuals were observed in vegetation away from the water.

For some species and sites numbers of males and females at the site of oviposition were very low, resulting in small sample sizes. To maintain a robust analysis, we have only included sites of species for which we obtained samples with 25 or more individuals (males + females) (except for one site of *N. rufostigma* that was included with N = 23). For all species where multiple estimates of ratios of males

to females could be obtained, we applied replicated G tests (Sokal & Rohlf 1994, p. 720). This approach not only provides an overall (pooled) test of whether such ratios in any given species deviate from a 1:1 ratio (through G_{POOLED}) but it also allows us to test whether departures from expectation are in the same direction and magnitude in the different populations where the data were collected (through $G_{HETEROGENEITY}$, equivalent to an interaction term in an analysis of variance). These two G statistics sum to G_{TOTAL}, a reflection of total divergence from expectation independent of the direction(s) of departure. Beatty *et al.* (2007) reports on basic environmental characteristics for all of the sites included here. This allows us to investigate whether island characteristics, elevation or habitat may explain patterns of male rarity.

Territoriality

Based on our surveys we identified three abundant *Nesobasis* species where males were relatively rare (*N. rufostigma*, *N. heteroneura* and *N. malcolmi*) (further referred to as 'female-biased' species) and three abundant species where females were relatively rare (*N. anguilicollis*, *N. erythrops* and *N. selysi*) (further referred to as 'male-biased' species, although we note that at some sites males and females were approximately equally common). Individuals from each of these species were the subjects of our focal observation study. Females of male-biased species (*N. anguilicollis*, *N. erythrops*, *N. selysi*) were rarely observed singly at the site of oviposition (usually they were seen while mating with a conspecific male). Furthermore, males of *N. rufostigma* and *N. malcolmi* were exceedingly rare. This meant that we could not make detailed replicated observations of the behaviour of the rarer sex of the above species when solitary. Note however that our behavioural observations still allowed us to test the central hypothesis, namely that females of female-biased species behave territorially, to such an extent that they behave like males of traditional species. Moreover, we were able to collect data on the behaviour of both solitary male and solitary female *N. heteroneura*, a female-biased species, and we were therefore in a position to test the prediction that females of this particular species show territorial behaviour while males do not.

Our focal observations were conducted in 2005. Observations of female *N. rufostigma*, of male and female *N. heteroneura*, and of male *N. anguilicollis*, *N. erythrops* and *N. selysi* took place on 24–26 August and 3 September at Nukunuku Creek (17°37.11′S, 177°56.71′E; 660 m asl), and on 7–9 September at Waikubukubu River (17°32.84′S, 177° 56.62′E; 210 m asl). *Nesobasis malcolmi* females were observed on 1 October at Vereni Creek in Abaca National Park (17°46.41′S, 177°37.46′E; 535 m asl) (note that this species was found only at this

one locality during our study). All observations were made between 09h00 and 16h00 local time on each of these days. On the first day at a site we initially captured and marked a large sample of individuals with unique alpha-numeric codes on their wings (using a waterproof pen). This marking was continued on subsequent observation days. We did not consider a marked individual for detailed observation until at least 1 h after release.

Focal individuals were chosen at random (with the proviso that they had not been observed before). Typically, due to our prior capture and mark efforts, these individuals already had a unique mark on their wings. If not, after an observation trial we attempted to capture the focal individual for marking. If we did not succeed in catching the unmarked focal individual, the observational data were not used for analyses, to prevent repeated observation of the same individual. Observations were performed with the naked eye and close-focusing binoculars whenever necessary, with the observer remaining within 2–3 m of the study organism, without casting a shadow near it.

We tested whether males and females demonstrated territorial behaviour by conducting repeated 15-min focal observations. In so doing, we assessed if, and how, focal individuals responded to natural intruders and we examined the degree to which they remained in a localized area. First, we recorded all cases in which the focal individual came within approximately 50 cm of a non-focal individual (a result of one or both individuals moving closer to one another), hereafter referred to as a 'potential interaction'. Potential interactions could eventually result in (1) both individuals ignoring one another ('no response') for the entire time they were within this proximity (2) the focal individual chasing (rapid active pursuit) the non-focal individual (with or without an aerial fight) – 'focal aggression' or (3) the non-focal individual chasing the focal (with or without an aerial fight) – 'non-focal aggression'. We then analysed separately the proportion of total potential interactions of a focal individual that were aggressive and initiated by the focal individual ('focal aggression') and the proportion of the total potential interactions for which there was no response (which we considered to represent mutual 'non-aggressive' behaviour). As territorial organisms tend to defend a particular discrete area we noted movements of 1 m or greater made by the focal individual that were directed away from the site of initial observation. These movement distances were always in relation to the site of initial observation such that the total represents the total distance away from the initial site at the end of the 15-min observation. We predicted that if males of traditional species and females of female-biased species were territorial and defended a specific site, then they would not only behave aggressively towards intruders, but that they would stay relatively close to the point of initial observation.

Table 1. Counts and male proportions (males/(males + females)) in species populations of *Nesobasis* where N ≥ 25 individuals were collected. Not all species here included have been formally described, which explains our use of a combination of species names and coding (such as *N.* sp. a, *N.* sp. l, *uds2*) to refer to species (see Beatty *et al.* 2007 for more details). P-value refers to tests of whether the numbers of males and females at the site differed significantly from a 1:1 ratio (based on G-test for homogeneity with 1 df). Site descriptions and latitude/longitude for the majority of our sampling sites are provided in Beatty *et al.* (2007).

Species	Island	Site name	Year	Males	Females	Proportion	P-value
N. sp. a	Vanua Levu	Raviravi	2005	18	9	0.67	0.0803
	Vanua Levu	WR-01	2006	11	14	0.44	0.548
	Vanua Levu	KR-01	2006	18	11	0.62	0.191
	Vanua Levu	KR-02	2006	14	28	0.33	0.0292
N. anguilicollis (Tillyard)	Viti Levu	AR-03	2005	22	11	0.67	0.0532
N. brachycerca (Tillyard)	Vanua Levu	Raviravi	2005	25	2	0.93	<0.0001
	Vanua Levu	WR-01	2006	99	4	0.96	<0.0001
	Vanua Levu	KR-01	2006	70	8	0.90	<0.0001
	Vanua Levu	KR-02	2006	41	0	1.00	<0.0001
N. comosa (Tillyard)	Viti Levu	AR-03	2005	26	24	0.52	0.777
	Viti Levu	Wainikovu	2005	10	35	0.22	0.0001
N. erythrops (Selys)	Viti Levu	AR-03	2005	22	15	0.59	0.248
	Viti Levu	Waikubukubu	2005	42	18	0.70	0.0017
	Viti Levu	Wainivesi	2005	29	19	0.60	0.147
N. heteroneura (Tillyard)	Viti Levu	Nukunuku	2005	1	37	0.03	<0.0001
	Viti Levu	Waikubukubu	2005	8	29	0.22	0.0004
	Viti Levu	Wainivesi	2005	27	33	0.45	0.438
	Ovalau	Lovoni	2006	10	32	0.24	<0.0001
N. sp. l	Vanua Levu	Raviravi	2005	48	28	0.63	0.0210
	Vanua Levu	WR-01	2006	44	15	0.75	0.0001
	Vanua Levu	KR-01	2006	21	4	0.84	0.0004
	Vanua Levu	KR-02	2006	66	9	0.88	<0.0001
N. malcolmi (Donnelly)	Viti Levu	AR-03	2005	0	33	0.00	<0.0001
N. recava (Donnelly)	Kadavu	TR-01	2006	27	0	1.00	<0.0001
	Kadavu	Vunisea East	2006	62	3	0.95	<0.0001
N. rufostigma (Donnelly)	Viti Levu	Nukunuku	2005	0	29	0.00	<0.0001
	Viti Levu	VDR-02	2005	0	30	0.00	<0.0001
	Viti Levu	Waikubukubu	2005	0	29	0.00	<0.0001
	Viti Levu	Wainivesi	2005	0	31	0.00	<0.0001
	Ovalau	Lovoni	2006	0	23	0.00	<0.0001
N. selysi (Tillyard)	Viti Levu	VDR-02	2005	27	1	0.96	<0.0001
N. sp. t	Vanua Levu	Lomaloma	2005	13	23	0.36	0.0934
Uds 2	Vanua Levu	Volivoli	2005	74	27	0.73	<0.0001

Female activity

We conducted replicated 5-min focal trials to quantify the distribution of activities of females in the female-biased species when at the water (*N. rufostigma*, *N. heteroneura* and *N. malcolmi*). To do this, we simply estimated the proportion of the 5-min periods that females spent engaged in three mutually exclusive behaviours: flying, perching and ovipositing.

RESULTS

Male rarity

Analysis of all sites of all species indicated significant among-species variation in the ratio of males to females (Kruskal–Wallis test, $\chi^2_5 = 29.9$, P = 0.003). While in some species males were a common sight, outnumbering females at the water, in other species males were rare to absent (Table 1). For example, in *Nesobasis malcolmi* and *N. rufostigma* very few males (if any) were observed. By contrast, sex ratios in *N. erythrops* were all male-biased (Table 1). Eleven out of the 13 species had ratios of males to females that diverged significantly from 1:1 (Tables 1 and 2). While a number of the species were abundant at a single study site, other species (such as *N.* sp. a, *N. brachycerca*, *N. erythrops*, *N.* sp. l and *N. rufostigma*) were abundant at several sites (Table 1).

In *N. erythrops* and *N. rufostigma*, sex ratios were homogeneous across sites (Table 2). By contrast, *N.* sp. l showed between site variation ranging from slightly to strongly male-biased. Interestingly, *N.* sp. a, *N. comosa* and *N. heteroneura* also showed variation in such ratios between sites, from approximate equality to female-biased. Indeed, in *N. heteroneura* ratio of males to females ranged from 1 male and 37 females to 27 males and 33 females, while for *N. comosa* this was from 10 males and 35 females to 26 males and 24 females. Sex ratios in *N.*

Table 2. Results of replicated G-tests on *Nesobasis* species observed at different sites testing whether (1) male to female ratios deviated significantly from 1 to 1 (through G_{POOLED} and G_{TOTAL}) and (2) whether male to female ratios differed significantly among sites for each species (through $G_{HETEROGENEITY}$). Degrees of freedom are shown in parentheses. Please note that not all species here included have been formally described, which explains our use of a combination of species names and coding (*N.* sp. a, *N.* sp. l) to refer to species (see Beatty *et al.* 2007 for more details).

Species	Male or female bias	G_{POOLED}	P	$G_{HETEROGENEITY}$	P	G_{TOTAL}	P
N. comosa	Female	5.62 (1)	0.017	9.17 (1)	0.002	14.8 (2)	0.0006
N. heteroneura	Female	42.6 (1)	<0.0001	26.3 (3)	<0.0001	68.8 (4)	<0.0001
N. rufostigma	Female	197 (1)	<0.0001	0.00 (4)	1.00	197 (5)	<0.0001
N. sp. a	No bias	0.008 (1)	0.93	9.87 (3)	0.0017	9.88 (4)	0.043
N. recava	Male	101 (1)	<0.001	2.13 (1)	0.14	103 (2)	<0.001
N. brachycerca	Male	237 (1)	<0.0001	8.12 (3)	0.044	246 (4)	<0.0001
N. erythrops	Male	11.8 (1)	0.0006	1.55 (2)	0.46	13.3 (3)	0.004
N. sp. l	Male	67.7 (1)	<0.0001	14.13 (3)	0.0027	81.8 (4)	<0.0001

sp. a ranged from 14 males and 28 females to 18 males and 9 females.

Four of the species of *Nesobasis* here presented show male rarity at sites. *Nesobasis rufostigma* is a species that was found at most localities where *Nesobasis* spp. were present. The same is true for *N. heteroneura* in combination with *N. comosa*, where the latter is found at higher elevations compared to the former (Beatty *et al.* 2007). *Nesobasis malcolmi* was only found at one site at higher elevation. *Nesobasis rufostigma* and *N. heteroneura* were found both at Viti Levu and Ovalau where they showed male rarity on both islands. The widespread occurrence of male rarity indicates that it cannot be associated to specific island or site characteristics.

Territoriality

The total number of 'potential interactions' per focal individual did not differ significantly among species (Kruskal–Wallis test: $\chi^2_5 = 7.65$, P = 0.18). However, focal females of female-biased species and males in male-biased species showed significant differences in the proportion of potential interactions that resulted in focal aggression (Kruskal–Wallis test: $\chi^2_5 = 41.6$, P < 0.001, Figure 1a, b), with males demonstrating far higher proportions of interactions that resulted in aggressive behaviour. Likewise, females of female-biased species engaged in proportionately more non-aggressive encounters than males of male-biased species (Kruskal–Wallis test: $\chi^2_5 = 45.8$, df = 5, P < 0.001). Non-focal aggression, i.e. aggression initiated by the non-focal individual, was uncommon, with numbers too low to allow testing for differences. Species also differed significantly in the cumulative (>1 m) distances that individuals travelled from the point of initial observation (Kruskal–Wallis test: $\chi^2_5 = 25.0$, P < 0.001), indicating that males were more likely to remain in a discrete locality compared with females that covered larger distances (Figure 1c).

For *N. heteroneura* both single females and single males were observed (note that males of this species were not included in the above analyses). Ratios of males to females were substantially different between Nukunuku Creek (1 male and 37 females) and Waikubukubu River (8 males and 29 females) (Table 1), although both ratios were strongly female-biased. This allowed us to evaluate whether the tendency to exhibit territorial behaviours by males or females differed between the sexes and with the ratio of males to females. The total number of potential interactions per focal individual over all sites did not differ between males and females of *N. heteroneura* (Mann–Whitney U = 30.0, N = 21, P = 0.085), nor between the different sites irrespective of sex (Mann–Whitney U = 30.0, N = 21, P = 0.267). Ignoring location, males of *N. heteroneura* were involved in a significantly higher proportion of aggressive interactions compared to females (Mann-Whitney U = 10.0, N = 21, P = 0.001; Figure 1d). Exploring differences within sites, the proportion of focal aggressive interactions was significantly higher for males compared to females at Waikubukubu River (Mann–Whitney U = 3.5, N = 15, P = 0.002). While too few observations were taken at Nukunuku Creek to provide a valid test (N = 6 focally observed individuals in total, of which 3 were males and 3 were females), males similarly showed proportionately more aggressive interactions at this location.

Female activity

Female *N. malcolmi* (N = 8 observed individuals) and *N. rufostigma* (N = 8) spent most of their time at the water ovipositing (estimated mean 84% and 70% of their time during 5 min of observation, respectively), while female *N. heteroneura* (N = 10) spent only 28% of their time ovipositing. These interspecific differences in the estimated proportion of time focal individuals spent ovipositing were significant (Kruskal–Wallis test: $\chi^2_5 = 9.88$, P = 0.007). While watching females ovipositing on repeated occasions we observed females of the female-biased species ovipositing next to conspecific and heterospecific females without any form of interaction.
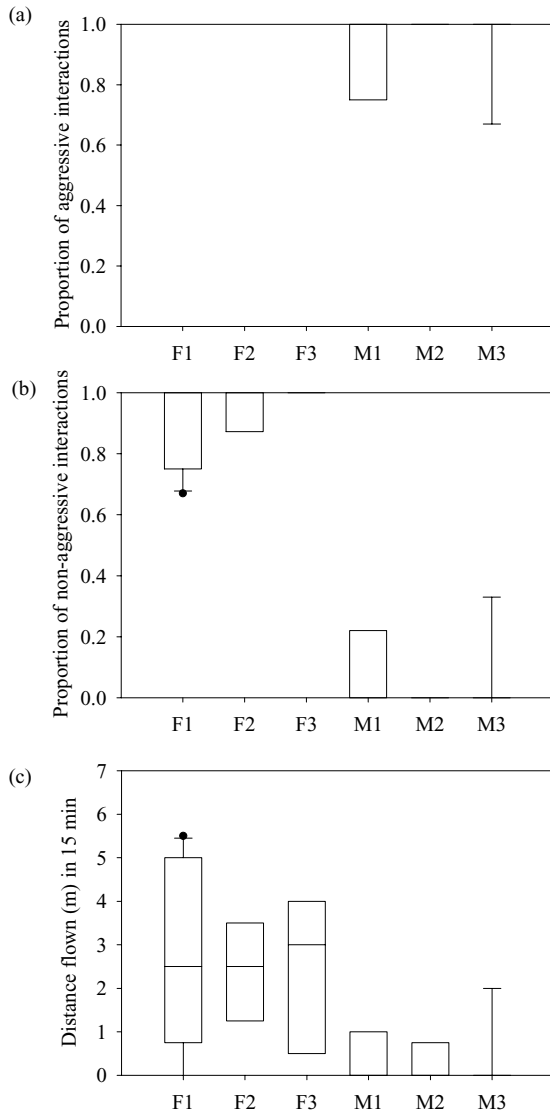
Figure 1. Interactions and distances moved in our focal observation studies for *Nesobasis* species on Fiji. In all cases, the line within the box represents the median, while the upper and lower boundaries of the box represent the 75th and 25th percentiles, respectively. The extent of the upper whisker represents the 90th percentile, while the extent of the lower whisker represents the 10th percentile. Dots represent any observations outside of these ranges. Data are provided for females in three female-biased species *N. heteroneura* (F1), *N. malcolmi* (F2) and *N. rufostigma* (F3) and males in three male-biased species (*N. angulicollis* (M1), *N. erythrops* (M2) and *N. selysi* (M3). Proportion of the total potential interactions that were aggressive (a). Proportion of the total potential interactions observed during our 15-min focal studies in which no response occurred (considered 'non-aggressive' interactions) (b). Sum of distances (>1 m) travelled during 15-min observations (c).

DISCUSSION

Male damselflies typically outnumber females at the site of oviposition (Corbet 1999, Hamilton & Montgomerie 1989) which is also seen for many of the species

of *Nesobasis* studied here. However, in support of the suggestions by Donnelly (1990), males are rare to absent in certain species, in particular *N. malcolmi* and *N. rufostigma*. Two other species, namely *N. comosa* and *N. heteroneura*, showed interesting between-site variation in the ratio of males to females, from near equality to strongly female-biased. Male rarity may generate unusual behaviour, such as lekking in female butterflies (Jiggins *et al.* 2000) or weak female territorial behaviour in experimentally manipulated dragonfly populations (Jacobs 1955). While we found male rarity at the water for some species, we however did not find support that females of these species exhibit territorial behaviour as was earlier suggested (Donnelly 1990), and as might be expected if females were forced to compete for mates. Even in the absence of territorial sex-role reversal, females may occasionally need to compete for access to quality oviposition sites. However, we frequently observed females at high density female-biased sites ovipositing immediately next to one another, suggesting that oviposition substrate availability is not a limiting factor for these females.

Therefore, while males of male-biased species (*N. erythrops*, *N. selysi* and *N. anguilicollis*) showed every indication of territorial behaviour (challenging intruders and occupying a discrete spatial location), females of female-biased species (*N. rufostigma*, *N. heteroneura* and *N. malcomi*) did not. In addition, males of *N. heteroneura* behaved in a more territorial manner than females, despite being the rarer sex. On one occasion we observed a male *N. heteroneura* consecutively courting five conspecific females; in all cases females rejected the male. This suggests a situation contrary to that observed with *A. encedon* (Jiggins *et al.* 2000), in that *N. heteroneura* females are not awaiting the occasional male to show up for mating.

Collectively, our results indicate that females in locations where they are the most common sex are not behaving like males, and that males and females continue to exhibit traditional roles from an odonotalogical perspective, independent of male rarity. Perhaps male rarity has not provided sufficient selection pressure to generate territoriality in females. Alternatively male rarity could be too recent a phenomenon on an evolutionary timescale to have generated a female territorial response. Of course it is possible that males in female-biased species may occupy unusual habitats away from the water where mating takes place, yet despite repeated searches away from streams we never located any male 'hotspots'. Indeed, as noted above, males of the female-biased species *N. heteroneura* actively defended territories at the water and solicited matings, a behaviour more in line with mating occurring at the water rather than at an alternative location. Even if males of female-biased species were simply residing elsewhere,

then we would still need to explain why more males were not seeking to intercept females at the water, as seen in the vast majority of damselflies worldwide. Extreme monandry is one possibility; in which males focus their efforts on mating with newly emerged females at a time of day or location that is not easily observable (Robinson & Allgeyer 1996, Tillyard 1917).

Besides the above explanation, several other theories for male rarity at oviposition sites are currently being investigated. One intriguing possibility is that some species of *Nesobasis* are infected with intracellular parasites, such as *Wolbachia*, that selectively kill males at some stage in their life cycle, or induce parthenogenesis (Stouthamer *et al.* 2002) – indeed *Wolbachia* has been recently found in several species of *Nesobasis* (Charlat *et al.*, unpubl. data). The first and only known example of parthenogenesis in damselflies, in populations of *Ischnura hastata*, has also been seen on a remote archipelago – in this case the Azores (Belle & Van Tol 1990, Cordero-Rivera *et al.* 2005, see also Sherratt & Beatty 2005). It is possible that male-killing parasites are not as strongly selected against during the colonization of remote islands where finding mates is difficult. Alternatively, or in addition, parthenogenesis can also result from hybridization of newly arrived colonists with established species (Cuellar 1977, Kearney 2005, Vandel 1928). The occurrence of male rarity then would not directly relate to differences in environment between sites within Fiji, but may relate to differences between islands in general and the mainland. Intriguingly, an ongoing species-level phylogeny indicates female-bias at aquatic oviposition sites in *Nesobasis* has evolved multiple times (unpubl. data).

While we continue to pursue the proximate and ultimate causes for the within and between species variation in male rarity in the genus *Nesobasis*, we have formally quantified the remarkable variation in the abundance of the sexes in over a dozen separate species, and determined through direct observation that male rarity at the oviposition site is not associated with behavioural sex-role reversal. Whatever factors may explain variation in male rarity among species of *Nesobasis*, we think this tropical system holds great potential for questions on island ecology and evolution, speciation, and the evolution of mating systems in general. Many regions of the tropics, especially the islands of the South-West Pacific remain largely unexplored from the standpoint of odonate diversity and ecology (Donnelly 1990), and more work is needed if we are to preserve these unique communities.

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