

Sex biases in dispersal and philopatry: insights from a meta-analysis based on capture–mark–recapture studies of damselflies

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Sex-biased dispersal is well known for birds and mammals, typically by females and males, respectively. Little is known about general patterns of sex-biased dispersal in other animal taxa. We reviewed return rates for a model group of invertebrates (damselflies) and explored putative costs and benefits of dispersal by males and females. We used published capture–mark–recapture data and examined whether a sex bias existed in likelihood of recapture at least once, at both emergence and/or breeding sites. We assessed whether this metric of likelihood of recapture was indicative of dispersal or philopatry, and whether any emerging pattern(s) were consistent across damselfly families. Using a meta-analysis, we found a higher likelihood of recapture at least once for males than for females at both natal sites and breeding sites, which seemed attributable to higher female-biased dispersal, although female-biased mortality cannot be discounted particularly for some species. Sex biases in dispersal among damselflies may be understood based on sex differences in maturation rate and foraging behaviour, both of which should affect the costs and benefits of dispersing. This hypothesis may be useful for explaining patterns of dispersal in other animal taxa.

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Dispersal can be defined as a one-way movement of organisms from one home site to another, whereas philopatry can be defined as exhibiting a tendency to remain in the native locality (*sensu lato* Lincoln et al. 1998). Dispersal and philopatry are central to the biology of most organisms because of their influences on schedules of survivorship and reproduction. These schedules underpin demographics that can influence both population dynamics and population genetics (Sugg et al. 1996).

One longstanding issue in animal ecology and evolution is sex differences in dispersal and/or philopatry, which have received attention mainly from researchers studying birds and mammals. In these two animal

groups, general patterns have been identified: typically, dispersal is female-biased for birds and male-biased for mammals (reviewed by Greenwood 1980, Dobson 1982, Clarke et al. 1997). Researchers have explored the functional significance of sex-biased dispersal in these groups of vertebrates by addressing the costs and benefits of dispersal for individuals of both sexes. For example, inbreeding avoidance is considered a key driver for dispersal (Waser et al. 1986, Perrin and Mazalov 1999); however, dispersal is required by only one sex to avoid inbreeding. Explanations for why individuals of one sex disperse more in a particular animal group, or are more philopatric, often rely more on specific details of mating systems under study, and/or how dispersal

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behavior affects expectations of future reproductive success for both males and females (Greenwood 1980, Dobson 1982, Caizergues and Lambrechts 1999).

There are many hypotheses for sex-biased dispersal that relate to sex differences in expected costs and benefits of dispersing. Typically, these hypotheses are founded on details of either avian or mammalian biology (e.g. resource defence of birds favouring philopatry by territorial males). Recently however, sex differences in philopatry and/or dispersal have been documented for several other animal taxa (e.g. fish: Hutchings and Gerber 2002, Bekkevold et al. 2004; amphibians: Austin et al. 2003; reptiles: Olsson and Shine 2003; and several species of invertebrates: Caudill 2003, Sundström et al. 2003). There is now a need to address sex-biased dispersal in these organisms. In particular, are general patterns apparent? Also, can we identify putative costs and benefits of dispersing by males and females that explain the observed patterns? To date, there has not been an attempt to explore general patterns of sex-biased dispersal and/or philopatry in taxa other than birds and mammals. Studies on non-avian and non-mammalian taxa will benefit from previous research done on birds and mammals. However, new or refined explanations may be required to explain sex biased dispersal in these other taxa, based on consideration of specific costs and benefits of dispersing by individuals of either sex.

In this study, we provide the first general study of sex biases in dispersal and/or philopatry across species of invertebrates. We use a meta-analysis to test sex differences in expectation of dispersal by damselflies (class Insecta, order Odonata, suborder Zygoptera). Our study is based on published capture–mark–recapture (CMR) data. Damselflies can be considered model invertebrates for studies on dispersal because they are relatively easy to handle and mark individually (Bohonak and Jenkins 2003), producing data equivalent to CMR studies on birds and mammals. Furthermore, because damselflies typically reproduce at ponds or streams, researchers can survey such well-delineated areas intensively and record returns by individuals. Additionally, emergence sites of these insects can be thought of as analogous to natal sites of birds and mammals, with emerging individuals typically leaving the natal site for a considerable period of time (maturation time) before settling for breeding, in either natal or non-natal areas.

Our study had several objectives. First, we addressed whether sex biases existed among different species of damselflies in the likelihood of being recaptured at least once after initial marking (or LR). We assessed whether any sex biases in LR occur at the natal site. We also compared these results to the magnitude of sex biases in LR for reproductively mature damselflies. Related to this objective, we tested if a correlation existed between sex biases in pre- and post-maturation dispersal among species. We further addressed the extent to which sex

biases in LR were homogenous across different species of damselflies belonging to different families, again controlling for maturation stage since this encompasses recapture at natal sites versus breeding sites. These tests are informative since different genera and families of damselflies are known to have different mating systems (e.g. ranging from territorial defence of oviposition sites to scramble mate competition, Corbet 1999). Contrasting species with different mating systems has helped identify explanations for differences in sex-biased dispersal and philopatry in birds and mammals (Dobson 1982, Clarke et al. 1997).

It is also relevant that some recent studies on damselflies have estimated survivorship of males and females separately from data on frequency of recaptures or recapture rates (Anholt 1997, Andrés and Cordero 2001, Anholt et al. 2001). This additional information is important because ascribing differences in likelihood of recapture to actual differences in dispersal can be difficult if differential survivorship is not addressed. A more detailed meta-analysis would include both recapture and survival rates to infer whether patterns in dispersal exist. Unfortunately, few studies make use of advanced analyses for CMR data (i.e. researchers separate survival from recapture probabilities). Performing meta-analysis simply on return rates or LR data, which are the best data currently available for damselflies, is a necessary and informative first step to assess whether patterns of sex-biased dispersal may exist and require explanation. As addressed below, we considered the best available information on sex-specific survival rates within damselfly species, to help formulate our arguments.

In summary, we provide a general test of sex differences in dispersal and/or philopatry for a non-avian and non-mammalian group of model organisms. Our analysis indicates a higher likelihood for males than females to be recaptured at least once after initial marking. This finding appears attributable to sex differences in dispersal from natal and/or breeding sites, although mortality differences cannot be discounted, particularly for some species. We complete our study by identifying an alternative explanation for this phenomenon following earlier research suggesting sex differences in age of first breeding and habitat use may influence dispersal (Johnson 1986). We reformulate this hypothesis in light of our findings on damselflies: this new explanation may have important bearing on understanding sex-biased dispersal in damselflies and possibly other animal taxa.

Methods

Relevant natural history of damselflies

Damselflies have both an aquatic larval stage and a terrestrial winged stage. The larval stage typically is long compared to the reproductive stage. After months to

years, the larvae emerge from the water as fragile winged adults, hereafter referred to as teneral. Tenerals must feed for a considerable period of time, ranging from about 4 days up to several weeks, before becoming reproductively mature adults (Corbet 1999). Mature damselflies make visits to a breeding site(s), interspersed with periods away from the site(s). This behaviour is analogous to breeding dispersal versus non-dispersal. It is important that researchers can distinguish teneral damselflies from mature adults, by the tenerals' fainter colouration and glistening wings (Corbet 1999). Discrimination between pre- and post-maturation adults allows for analysis of both pre- and post-maturation dispersal, based on recapture information.

For most damselfly species studied, males spend more time than females at the pond or stream during their reproductive period, while females usually only make visits when receptive (i.e. each time after they have mated a new clutch of eggs, Corbet 1999). If unreceptive, females typically forage away from the pond or stream, where males are less abundant. The interval between subsequent visits to the breeding site usually is longer for females. However, both males and females regularly visit stream or pond and also forage at and away from the water. Unfortunately, for many of the damselfly species in our study, detailed information on their reproductive ecology is lacking, which makes it impossible to ascribe mating systems to many species included in this study. We thus could not consider whether ecological factors act as moderating variables affecting degree of sex biases in LR. However as indicated above, we can test whether general patterns of sex biases in LR are apparent among species: some of which are known to vary considerably in their reproductive ecologies.

Data mining and meta-analytical approach

We searched the damselfly literature for CMR studies where individuals were marked as tenerals (newly emerged immature damselflies) and recaptured as mature adults (for natal dispersal), and for studies where individuals were both marked and recaptured as mature adults (for breeding dispersal). CMR studies had to meet five criteria in order to be included in our study. First and second, the study was published after 1960 and was either currently covered by the ISI Web of Science® database or appeared in *Odonatologica* – the longest running peer-reviewed international journal on odonate research. Third and fourth, damselflies had to have been captured and recaptured at the same water body (pond or stream), and the total number of individuals marked and recaptured had to be available for both sexes separately. Suitable studies for analysis were limited because complete information often was lacking, mostly with respect to these third and fourth criteria. Fifth,

researchers had to have sampled intensively at sites. This fifth criterion was of major importance because male damselflies typically have a higher likelihood of being recaptured more frequently than females due to sex differences in behaviour or possibly also conspicuousness (Anholt 1997, Corbet 1999).

Data were collated from a survey of different damselfly species from the families: Calopterygidae, Coenagrionidae, Lestidae, and Platystictidae (see Table 1 for a full list and details on CMR data of the representative species). Data based on return rates are the best data currently available for damselflies which allow for meta-analytical approaches. We recognise that these data only indirectly provide information about dispersal. Specific data on dispersal distance are scarcely published for damselflies – the few case studies that do measure dispersal distance are included in our arguments whenever appropriate. There is also another uncertainty with recapture data. Individuals marked only after maturation could have dispersed to that site from a foreign site, which is why we consider breeding and natal dispersal separately. For any individual marked and recaptured, a specific location may therefore represent both its natal and its breeding site, or only its natal site, or only its breeding site.

CMR data may also incorporate a sampling bias because sex differences in behaviour, habitat use and conspicuousness translates to males being seen more easily or frequently at the water than females. Long and intensive periods of sampling however, should guarantee the re-sighting of returning individuals, independent of sex (or conspicuousness) (Stoks 2001a). We thus only included studies in our meta-analysis that had intensive sampling over extended periods of time. More specifically, we included studies where researchers typically sampled daily, weather permitting, over periods ranging from 3 weeks to 3.5 months. As mentioned, we were only interested in whether an individual was recaptured at least once (LR), and not whether it was recaptured many or a few times. We believe that LR reliably indicates degree of dispersal or philopatry for a group of known individuals. Although male and female damselflies may differ in the number of times they are recaptured due to differences in behaviour or conspicuousness, this factor should not influence estimates of LR from intensive studies. However, there is still a concern of whether not being recaptured represents mortality or dispersal. To address this, we examined whether sex biases in LR occur consistently and is not simply reflective of what is known about sex biased mortality for species where estimates of survival rates have been obtained reliably for males and females.

In total, data were collated from 19 CMR studies for 18 species of damselflies (Table 1). More specifically, data were reported for both tenerals and mature adults of two *Palaemnema* species in one of these studies. In

Table 1. Published studies with capture–mark–recapture data of male and female damselflies used in our meta-analysis. The total number of individuals marked (n), and the proportion recaptured (% R), are reported for studies where individuals were marked as teneral (T) and/or mature adult (A), and separate for males (M) and females (F). These damselflies belong to four families: Calopterygidae (1), Coenagrionidae (2), Lestidae (3) and Platystictidae (4). Asymmetric confidence limits on recapture proportions were calculated using the Clopper-Pearson method (Zar 1984).

Age	Study species	Family	Sex	n	% R	Confidence interval	Ref*	
T	<i>Calopteryx haemorrhoidalis</i>	1	M	26	0.769	(0.564–0.910)	1	
			F	10	0.700	(0.348–0.933)		
	<i>Calopteryx splendens</i>	1	M	475	0.438	(0.393–0.484)	2	
			F	434	0.327	(0.283–0.374)		
	<i>Ceriagrion tenellum</i>	2	M	1045	0.169	(0.147–0.194)	3	
			F	845	0.130	(0.108–0.155)		
				M	911	0.167	(0.143–0.193)	4
				F	759	0.132	(0.109–0.158)	
	<i>Coenagrion puella</i>	2	M	1381	0.219	(0.197–0.241)	5	
			F	1333	0.128	(0.110–0.147)		
	<i>Enallagma boreale</i>	2	M	878	0.035	(0.024–0.050)	6	
			F	933	0.015	(0.008–0.025)		
				M	580	0.069	(0.050–0.093)	6
				F	565	0.046	(0.030–0.067)	
	<i>Enallagma hageni</i>	2	M	145	0.400	(0.320–0.485)	7	
			F	174	0.218	(0.159–0.287)		
				M	32	0.688	(0.500–0.839)	7
				F	38	0.421	(0.263–0.592)	
				M	14	0.429	(0.177–0.711)	8
				F	31	0.258	(0.119–0.446)	
	<i>Pyrrosoma nymphula</i>	2	M	76	0.316	(0.214–0.433)	9	
			F	72	0.250	(0.155–0.366)		
	<i>Lestes barbarus</i>	3	M	157	0.376	(0.300–0.457)	10	
			F	97	0.165	(0.097–0.254)		
				M	126	0.286	(0.209–0.373)	10
				F	109	0.183	(0.116–0.269)	
				M	67	0.209	(0.119–0.326)	10
				F	35	0.114	(0.032–0.267)	
	<i>Lestes disjunctus australis</i>	3	M	23	0.435	(0.232–0.655)	11	
			F	40	0.075	(0.016–0.204)		
	<i>Lestes virens vestalis</i>	3	M	142	0.183	(0.123–0.257)	10	
			F	121	0.017	(0.002–0.058)		
<i>Palaemnema desiderata</i>	4	M	42	0.286	(0.157–0.446)	12		
		F	40	0.375	(0.227–0.542)			
<i>Palaemnema paulitoyaca</i>	4	M	21	0.143	(0.030–0.363)	12		
		F	12	0.083	(0.002–0.385)			
A	<i>Calopteryx haemorrhoidalis</i>	1	M	83	0.831	(0.733–0.905)	1	
			F	28	0.786	(0.590–0.917)		
	<i>Calopteryx maculata</i>	1	M	212	0.660	(0.592–0.724)	13	
			F	160	0.494	(0.414–0.574)		
				M	148	0.507	(0.423–0.590)	13
				F	138	0.464	(0.379–0.551)	
	<i>Calopteryx splendens</i>	1	M	1068	0.487	(0.457–0.517)	2	
			F	672	0.271	(0.238–0.306)		
	<i>Argia apicalis</i>	2	M	202	0.718	(0.650–0.779)	14	
			F	113	0.407	(0.316–0.504)		
	<i>Argia chelata</i>	2	M	458	0.461	(0.414–0.508)	15	
			F	166	0.663	(0.585–0.734)		
	<i>Argia plana</i>	2	M	143	0.720	(0.639–0.792)	16	
			F	143	0.510	(0.426–0.595)		
	<i>Argia sedula</i>	2	M	584	0.317	(0.279–0.356)	17	
			F	149	0.128	(0.079–0.192)		
	<i>Ischnura gemina</i>	2	M	244	0.807	(0.752–0.855)	18	
			F	124	0.540	(0.449–0.630)		
				M	122	0.902	(0.834–0.948)	18
				F	73	0.521	(0.400–0.639)	
	<i>Lestes disjunctus australis</i>	3	M	91	0.824	(0.730–0.896)	11	
			F	74	0.581	(0.461–0.695)		
	<i>Lestes disjunctus disjunctus</i>	3	M	263	0.715	(0.656–0.769)	19	
			F	433	0.148	(0.116–0.185)		
	<i>Palaemnema desiderata</i>	4	M	808	0.728	(0.696–0.758)	12	
			F	368	0.590	(0.538–0.640)		
	<i>Palaemnema paulitoyaca</i>	4	M	133	0.489	(0.401–0.577)	12	
			F	34	0.265	(0.129–0.444)		

* Beukema (2002)¹, Schutte et al. (1997)², Andrés and Cordero (2001)³, Andrés and Cordero (1998)⁴, Banks and Thompson (1985)⁵, Anholt (1991)⁶, Fincke (1994)⁷, Fincke (1982)⁸, Bennett and Mill (1995)⁹, Utzeri et al. (1988)¹⁰, Bick and Bick (1961)¹¹, Garrison and Gonzalez-Soriano (1988)¹², Waage (1972)¹³, Bick and Bick (1965)¹⁴, Hamilton and Montgomerie (1989)¹⁵, Bick and Bick (1968)¹⁶, Robinson et al. (1983)¹⁷, Garrison and Hafernik (1981)¹⁸, Duffy (1994)¹⁹

each of two other studies, data were given for teneral and adults of a (different) *Calopteryx* species. In a fourth study, data were reported for teneral and adults of a *Lestes* species. A fifth study reported data for teneral adults of two *Lestes* species. For the remaining 14 studies, author(s) either reported results of studies on just individuals marked as tenerals of a single species (seven studies), CMR data of only mature adults of a single species (six studies), or adults of a recognized subspecies (one study). For those studies where only the number of individuals marked and the proportion recaptured was provided, the number recaptured was recalculated. If multiple CMR data for the same species were available, they were included in our analyses.

A meta-analysis was performed on the total data set. An effect size for each species or subspecies was estimated using the odds ratio (OR; Rosenthal 1994), where the strength of differences in marked (m) and recaptures (r) between males (M) and females (F) are summarized $OR = \ln(M_m F_r / M_r F_m)$. The odds ratio is commonly used for count data (such as CMR data) that have a binary factorial design (e.g. male versus female against marked versus recaptured), and has parametric properties necessary for heterogeneity tests and calculating of confidence intervals (Hedges and Olkin 1985). Mean OR across k studies was estimated using the Mantel-Haenszel method (hereafter the fixed effect model; Mantel and Haenszel 1959), and the random effect method (following DerSimonian and Laird 1986). Each model weights studies by their inverse variance. They differ in that the fixed effect model statistically assumes that there exists a common effect across all studies when weighting studies (e.g. the odds ratio should be similar for each study), whereas the random model assumes that each study may have a different odds ratio effect.

The heterogeneity test (Q test; details in Hedges and Olkin 1985) determines which effect model may be more appropriate for the data, by determining the extent of variation in effects between studies that could not be explained by sampling error alone (Hedges and Olkin 1985). More specifically for our purposes, heterogeneity statistics also can be used to test differences between moderator groupings (e.g. taxon) by contrasting Q test results between groups with overall Q tests (a method analogous to analysis of variance; Hedges and Olkin 1985). Means of fixed and random effects, their respective 95% confidence intervals (CI), and Q tests were calculated using the rmeta package of R (version 2.0.0; Ihaka and Gentleman 1996).

One inherent bias of meta-analysis is that studies with non-significant results are underrepresented in the literature. However, for most of the studies included in our analysis, the focus was not on sex biases in chances of at least one recapture (LR). Thus, the likelihood of publication bias was not determined by the strength of

magnitude in differences in LR found between sexes. Theoretical expectations may also drive publication of results, as suggested recently by another meta-analysis that takes into consideration timing of development of hypotheses and models, relative to publications based on empirical data (Leimu and Koricheva 2004). To date, there has not been formal theory attempting to predict sex biases in dispersal for damselflies.

Results

Overall, males were more likely to be recaptured at least once (had higher LR) than females (Table 2), although there was large variation in effect sizes across these studies (a significant overall Q test for heterogeneity; Table 2). These results suggest further analysis of moderator effects. Parsing data into teneral and mature adult groupings did not change overall direction of effects, where males again had higher LR, irrespective of maturity class (Table 2). Thus, males were more likely to be recaptured at natal sites and breeding sites than were females and mature males were more likely to be recaptured than teneral males ($Q = 21.2$, $df = 1$, $p < 0.001$). However, in both maturity classes there again existed variation in effects between studies that could not be explained by sampling error alone (significant Q tests for teneral and mature adults; Table 2). When only considering data for teneral damselflies (recapture at emergence sites), families of damselflies differed significantly in effect (between family contrast: $Q = 10.6$, $df = 3$, $p = 0.014$). This result is due to platystictid tenerals not showing an overall difference between males and females in LR whereas all other families maintained significantly higher LR for male than for female tenerals (Fig. 1). For tenerals, there is no evidence that sex biases in LR varied strongly within family (within family contrast: $Q = 22.5$, $df = 14$, $p = 0.069$); thus, much of the variation in effect sizes measuring sex biases in LR is explained by family. In other words, sex differences in LR are relatively homogenous within families when considering recaptures at emergence sites.

For mature adult damselflies or recapture at breeding sites, this homogeneity was not the case. Although family again accounted for variation in sex biases in LR assessed using effect sizes (between family contrast: $Q = 84.3$, $df = 3$, $p < 0.001$), there was also a significant within family contrast ($Q = 117.8$, $df = 10$, $p < 0.001$). Thus, taxonomy (family) was insufficient to explain remaining variation in sex-biased LR for mature adults assessed at breeding sites, although for all families considered, LR was significantly male-biased.

We did not find a correlation in magnitude of sex biases in pre- and post-maturation LR among species, where both types of effect sizes could be calculated ($N = 7$, Spearman $R = 0.32$, $p = 0.48$).

Table 2. Meta-analysis of capture–mark–recapture data for male and female damselflies. The mean odds ratio (OR) effect size for the fixed effect model was calculated using the Mantel and Haenszel (1959) method, and the random effect model following DerSimonian and Laird (1986). An OR >1.0 indicates males had greater chances on recapture than females, whereas an OR <1.0 indicates the opposite (females recaptured more often). Confidence intervals (95% CI) for effect sizes that do not overlap with 1.0 indicate a significant difference between male and female recapture proportions ($p < 0.05$).

	Model	OR	95% CI	Q (p) *
All studies (k = 32)	fixed	2.044	(1.898–2.201)	256.4 (<0.0001)
	random	2.268	(1.778–2.893)	
Teneral adults (k = 18)	fixed	1.723	(1.551–1.915)	33.1 (0.0109)
	random	1.813	(1.506–2.181)	
Mature adults (k = 14)	fixed	2.418	(2.180–2.683)	202.1 (<0.0001)
	random	2.622	(1.667–4.125)	

*df = k – 1

Discussion

Our study provides evidence of the following: in general, male damselflies are more likely than conspecific females to be recaptured at least once, both at natal sites and breeding sites. However, there exists variation in the magnitude of this sex bias between families (and within families for mature adults). We address the implications of our main findings below. We begin by addressing the extent to which this sex difference in LR may be explained, at least in part, by sex differences in dispersal tendency (versus considerations of differential mortality).

CMR data provide information on whether (and how often) individuals are re-sighted after being marked. Initial studies on survival faced the problem that differences in recapture rates between males and females could not, with certainty, be attributed to actual differences in survival. This was especially a problem for studies on damselflies because adult males return to the water (i.e. mating site) more frequently than females

(Corbet 1999), and thus have greater recapture frequencies (Anholt 1997). Recent advances in CMR modelling enable researchers to separate estimations of survival and recapture rates (Lebreton et al. 1992). Studies on damselflies applying these techniques support the absence of differences in survival between mature adult males and females in natural populations (Anholt 1997, Andrés and Cordero 2001, Anholt et al. 2001). While inferences on sex differences in survival assume that individuals have died after last recapture, it is however equally plausible that if an individual was not recaptured again, it may have dispersed.

With respect to teneral adults not yet reproductively mature, much less is known about possible differences in survival between sexes (Stoks 2001b, Andrés and Cordero 2001). This life stage, however, is particularly important because it is thought to be the stage when dispersal occurs primarily (Banks and Thompson 1985, Corbet 1999). A higher tendency to disperse during maturation is intuitive considering the details of damselfly biology. Adult damselflies not yet reproductively mature often differ in habitat use from those that are mature. While mature adults spend more time at the water, typically, teneral individuals of both sexes forage away from the water during the maturation period (an exception to this general rule are members of the genus *Ischnura*; Corbet 1999, Anholt et al. 2001). Several researchers have argued that because female damselflies in general have longer maturation times (Corbet 1999), they should experience a higher likelihood of mortality than males (Anholt 1997, Stoks 2001b). Teneral females also need to increase mass nearly twice as much as males due to maturation of the ovaries (Anholt et al. 1991). As a result, teneral females have longer foraging times than males, which may expose them to greater predation risks, but such remains unsupported (Stoks 2001b). Alternatively, or in addition, females possibly have increased chances for dispersal compared to males during this maturation period (details below).

Sex differences in survivorship could contribute to the magnitude of sex biases in LR as reported in our study. However, current studies on damselflies do not unequivocally support lower mortality rates for adult or

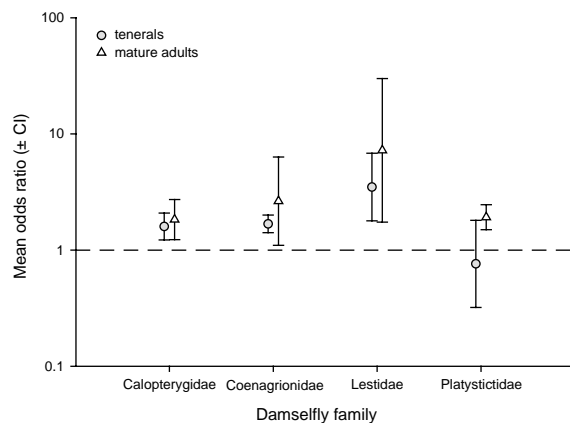


Fig. 1. Mean odds ratio effect sizes and their 95% confidence intervals (CI) for the random effect model (DerSimonian and Laird 1986) on a semi-logarithmic scale. Mean effect sizes are shown separate for studies where individual damselflies were marked as tenerals or as adults, for all four families included in our study. The dashed line with equation $y = 1.0$ indicates the level above which male chances on recapture are higher, and below which female chances on recapture are higher.

maturing males. If survivorship in many cases is similar for males and females, then we should often find instances of no overall differences in LR between the sexes. Because we do find rather consistent and strong sex biases in LR, we suggest that general differences in dispersal exist between sexes. Of course, one of the costs generally ascribed to dispersal is a higher mortality (Perrin and Mazalov 2000).

Traditionally, generalisations on sex biases in dispersal and philopatry of mammals and birds invoke differences in mating system as a key factor for discrepancies between these two taxa (Greenwood 1980, Dobson 1982). While information on mating systems of many species of damselflies unfortunately is unavailable, clearly, variation is present. Our study includes species where the respective authors consider males to be territorial (e.g. genus *Calopteryx*, some *Argia* spp.) and species with scramble mate competition where males sometimes guard mates until oviposition (e.g. *Lestes barbarus*, *Lestes virens vestalis*), and yet other species do both (Corbet 1999). It is interesting that we found significantly higher LR for males in both territorial species and non-territorial species showing scramble mate competition. For all damselfly species so far studied, competition for mates seems strongest for males, regardless if the species is territorial or not. Following the mate defence hypothesis proposed for mammals, males should then be the sex to have a lower recapture likelihood (Greenwood 1980), which is opposite to what we find here.

Johnson (1986) alternatively proposed that the dispersing sex could be the one with the greatest delay in age at first breeding. This hypothesis seems appropriate for damselflies. Teneral female damselflies have a longer maturation period and typically avoid streams or ponds during this stage. They may, as mentioned earlier, also increasingly wander further away from these sites while foraging (Conrad et al. 2002). Females should thus have a higher chance than males to locate suitable breeding habitats other than their natal pond or stream. As adults, males and females also show differential habitat use. While males mostly remain at the water, females need to mature new clutches of eggs (Corbet 1999) and again may wander and forage further than males, away from their natal streams or ponds (Conrad et al. 2002). Furthermore, excessive male harassment could drive non-receptive females away from the pond, further reinforcing the likelihood of female wandering. The suggestion that female damselflies are more likely to disperse has been raised before (Utzeri et al. 1988, Conrad et al. 1999). While some studies indicated that females were more mobile (Bennett and Mill 1995, Conrad et al. 2002), other studies based on different species indicate the opposite (Duffy 1994), or simply had too small samples of recaptures for a conclusive interpretation (Conrad et al. 1999). In those few studies

where multiple sites were monitored simultaneously for dispersing individuals, females appear to disperse more than males (Conrad et al. 2002, Angelibert and Giani 2003; but see Geenen et al. (2000) for a CMR-study on *Lestes viridis* in which neither sex appears to disperse). Thus, we suggest that costs (harassment near to rendezvous sites) and benefits (more efficient foraging away from such sites) may lead to the expectation of greater female dispersal in most damselflies: an expectation consistent with our results.

We can also compare costs and benefits to males. In birds, the putative advantage for male philopatry is familiarity with territories (Greenwood 1980). Males of some damselfly species may be philopatric to gain resources necessary for copulations with receptive females, and there may be a premium on returning to such resources fast, rather than dispersing to other potential territories (which might explain low breeding dispersal in males of such species). However, males of many damselfly species are non-territorial (Corbet 1999). Hence, we may expect to see reduced benefits of natal or breeding site fidelity for males of such species, but we found high male recapture rates at natal ponds. One important point is that, in damselflies, males are time minimizers, whereas females are energy maximizers (Anholt et al. 1991). We hypothesize that males need not go far away from natal or breeding sites to secure resources for territorial defence or mate searching and, if suitable breeding sites are dispersed, then males may return to natal or breeding sites to minimize time spent 'out of reproductive readiness'. For males, lifetime reproductive success is determined to a large extent by the number of visits made to breeding sites, and even more so by the number of copulations per visit (Stoks 2000). Thus, returning to the same sites, rather than dispersing to new sites, will likely maximize male lifetime reproductive success. For females, it is not visitation rate per se, but rather a rate in keeping with the number of clutches they can mature (Corbet 1999).

Taken together, we believe that male biases in LR are due to females wandering and consequently dispersing. We hypothesize that general differences between male and female damselflies in their tendency to disperse from natal sites or breeding sites follows from differences in maturation times and habitat use by foraging adults. We recognize that unexplained variation in the magnitude of sex-biased recaptures at breeding sites remains and that habitat attributes may influence dispersal tendencies in damselflies (as shown by Jonson and Taylor 2000), and possibly even lead to a greater magnitude of sex biases in dispersal. Notwithstanding, our general hypothesis may help explain sex-biased dispersal in other animal taxa, but such remains to be explored.

One particularly interesting approach would be to identify invertebrate species or taxa where sex differences in maturation time and foraging behaviour are either

absent or opposite, and where data on LR have been reported. We predict that no sex bias in dispersal or male-biased dispersal should be observed, respectively. To our knowledge, such data are unavailable for damselflies. However, it is interesting that for platystictid teneral, males and females did not show an overall difference in LR – the maturation biology of these species needs to be investigated or CMR studies done on these species perhaps in different localities where greater samples of recaptures are obtained. Also, some species show apparent male dispersal (*Argia chelata*, Table 1) – these species should also be reinvestigated. Such studies would provide suitable opportunity to test the generality of our proposed hypothesis, in a similar vein to studies that examined sex-biased dispersal in birds where females compete for territories (some Anatidae; Greenwood and Harvey 1982).

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