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Measuring dispersal in a metapopulation using stable isotope enrichment: high rates of sex-biased dispersal between patches in a mayfly metapopulation

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Dispersal affects a wide array of ecological and evolutionary processes, but has been difficult to estimate empirically. A ^{15}Nitrogen stable isotope enrichment technique was used to passively mark all developing *Callibaetis ferrugineus hageni* (Eaton) mayfly larvae in a beaver pond that had previously been shown to be a patch in a source-sink metapopulation. After enrichment during the larval stages, dispersal among ponds by adult females was demonstrated by the presence of unmarked females ovipositing in the labeled pond, and marked females in an unlabeled pond. Observed frequencies of marked females suggested incomplete mixing between ponds. In contrast, males rarely dispersed from their natal pond, which was consistent with the unusual mating system in this species – adult *Callibaetis* are short-lived, do not feed, and females are sexually receptive immediately after emerging from the larval habitat. The frequent dispersal demonstrated using the stable isotope technique was a critical component of the source-sink dynamic observed in this metapopulation, and further use of this technique will provide insights into patterns of dispersal in spatially structured habitats.

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Dispersal by organisms has long been recognized as a factor affecting a broad spectrum of ecological and evolutionary processes (Darwin 1859, MacArthur and Wilson 1967, Levins 1969, Brown and Kodric-Brown 1977). However, the influence of dispersal on these processes in natural populations remains poorly understood, largely due to practical limitations (Dieckmann 1999, Nathan 2001). Metapopulation theory recognizes the importance of dispersal among sub-populations by definition, and a large body of theoretical work has shown that the details of dispersal strongly influence both local (patch) and regional (metapopulation) dynamics (Harrison and Taylor 1997, Diffendorfer 1998, Thomas and Kunin 1999, Travis and French 2000).

Relatively few studies have directly estimated interpatch exchange rates of organisms (but see Doncaster et al. 1997, Thomas and Hanski 1997, Ricketts 2001). The problem is particularly acute for taxa that cannot be marked easily in large numbers or tracked through the environment (e.g. seeds, most invertebrates). In this study, a ^{15}N stable isotope enrichment technique (Hershey et al. 1993) was used to directly estimate dispersal rates between two patches in a source-sink metapopulation of the mayfly *Callibaetis ferrugineus hageni* Eaton. Understanding the extent of exchange of individuals among ponds is important in this system because local mayfly population growth rates varied from strong sinks to strong sources (local population growth rate,

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Lambda = 0.06–2.64), the local mayfly population growth rate was negatively associated with the density of trout predators, females did not oviposit selectively with respect to the presence of trout predators, and indirect estimates of dispersal strongly suggested net dispersal among ponds (Caudill 2002). Thus, without dispersal, the expected fitness of adult females would depend solely on the quality of their natal ponds, and local sink populations (those with growth rates below replacement) would probably become extinct.

Adult females have the greatest potential for dispersal among ponds in this species, and their natural history enabled dispersal between emergence and oviposition (effective or natal dispersal, Greenwood 1980) to be quantified using the enrichment technique. One pond was "labeled" by enriching it with ^{15}N (Hershey et al. 1993). Larval *Callibaetis* incorporated the ^{15}N during development by consuming enriched detritus and associated microcommunities. Subsequently, adult females were collected at the labeled and at a nearby unlabeled pond and examined for "marks" – enriched ^{15}N isotopic composition. The degree of exchange of mayflies was estimated from 1) the proportion of females ovipositing at the unlabeled pond that were marked and 2) the proportion of females ovipositing at the labeled pond that were unmarked. Females were predicted to frequently disperse between ponds, because local recruitment of larvae was not correlated to local emergence of adults (Caudill 2002, 2003), and the known biology of the genus as a fugitive taxon (Wiggins et al. 1980, Berner and Pescador 1988).

Dispersal of males between the two ponds was also quantified by examining males collected in mating swarms for ^{15}N enrichment. Several features of the mayfly mating system in general, and *C. f. hageni* in particular, suggested males would be more philopatric than females. Mayflies are unique among insects because they have two winged stages: the prereproductive subimago and the sexually mature imago (Needham et al. 1935, Edmunds and McCafferty 1988). Male imagos form aerial swarms, typically near visual markers, and female imagos fly into swarms and mate (Allan and Flecker 1989, Harker 1992). *C. f. hageni* males follow this sequence of behaviors and aggregate at the edges of ponds in aerial swarms to search for, and mate with, females. In contrast to most mayflies, female *C. f. hageni* mate precociously as winged subimagos immediately after taking flight from the aquatic habitat (Caudill 2002). After mating, females molt to the imago stage, are in the terrestrial environment for approximately two weeks while their eggs develop, and they do not feed during this period (Berner and Pescador 1988, Caudill 2002). Females lay eggs in a single pond during a single oviposition event and typically die on the pond surface ("spent females"). Adult males also do not feed, and nearly all swarm for a single day (Caudill 2002) using resources obtained in the larval stages (Needham et al. 1935, Edmunds et al. 1976). Hence, males were predicted to swarm at their natal ponds, rather than dispersing to other ponds because this behavior could increase resources available for swarming and reduce the risk of mortality associated with dispersal through the terrestrial environment. Furthermore, it was presumed that the natal pond provides a reliable source of emerging, sexually receptive females. Overall, the results demonstrated frequent dispersal among ponds by females, while nearly all males swarm at their natal pond.

Methods

Study ponds

Two beaver ponds in adjacent watersheds, Avery and Forest Service (FS) 401, of the 12 described in Caudill (2002) were used for the mark-recapture experiment (Fig. 1). The labeled pond, Avery, was a large fishless pond (4676 m^2), and had several large emergent sedge beds; the microhabitat where $> 83\%$ of *Callibaetis* lar-

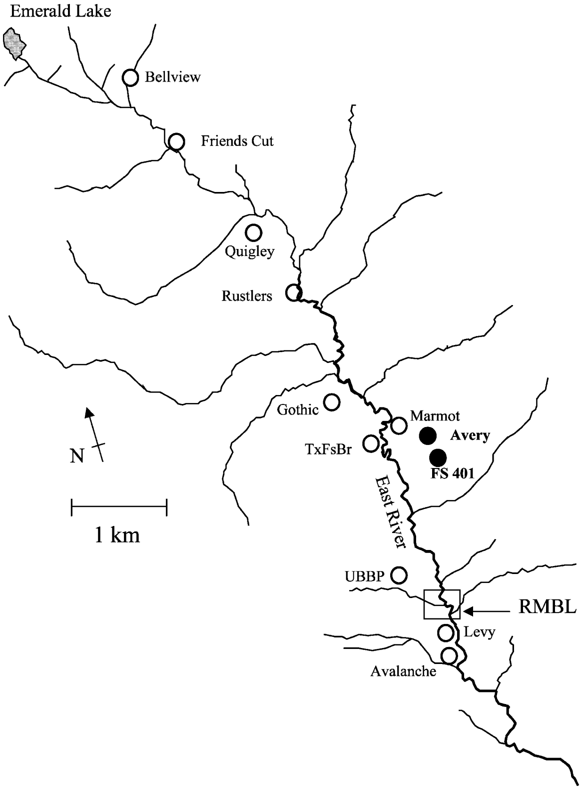


Fig. 1. Map of the East River drainage basin, Gunnison County, Colorado, and 12 ponds in the *Callibaetis* mayfly metapopulation near the Rocky Mountain Biological Laboratory (RMBL). The two ponds used in this study, Avery and FS 401, were separated by 250 m of typical sub-alpine spruce and open meadow (closed circles).

vae emerge (Caudill 2002). Avery was the largest and the terminal pond in a six pond complex. The upstream ponds varied from small (~ 500 m^2) to large (~ 3000 m^2) and had little emergent sedge habitat compared to Avery.

The unlabeled pond, FS 401 was 250 m southeast of Avery, and the two ponds were separated by a mix of spruce, montane meadow, and small stands of willow. FS 401 was smaller (991 m^2) than Avery and had an estimated density of 5.75 brook trout (*Salvelinus fontinalis*)/100 m^2 during the *C. f. hageni* larval growth period (Caudill 2002). Historically, FS 401 had been a fishless pond. Trout were introduced in September 1998 as part of an experiment to test how trout affect patch quality for *Callibaetis* larvae (Caudill 2002). FS 401 was the center pond of a five pond complex (with two additional ponds < 100 m^2). All five ponds in the complex were of similar size and had similar amounts of emergent sedge beds.

During summer 1999, the densities of last instar larvae and the areas of microhabitat within each pond were used to estimate the number of adults emerging from each pond (Caudill 2002). Avery was selected for the ^{15}N addition because of the large larval population observed there in the previous year (Caudill 2002). During the stable isotope mark-recapture experiment, an estimated 332 700 mayflies emerged from the pond, which was high compared to emergence from other ponds in the drainage basin (15.2% of the mayflies emerging from all 12 ponds, Caudill 2002). Far fewer, an estimated 26 400, adult mayflies emerged from FS 401 during the study period (Caudill 2002).

Stable isotope addition and sample collection

Five grams of ^{15}N enriched ammonium chloride (Isotech, Inc., minimum 99% atom % ^{15}N) was added to Avery using a 10 l hand pump bug sprayer (Rubbermaid, Inc.) on two dates (3 and 7 June 1999). One half was applied to the entire pond surface each day to minimize spatial variance in enrichment. The addition amount was estimated using data from Hershey et al. (1993). The amount of N added (0.294 mg m^{-2}) was probably small compared to other pools of nitrogen within the pond (Naiman et al. 1994).

Oviposition rates (females pond^{-1} day^{-1}) at each pond were estimated by collecting all spent females from the entire surface of both ponds on several dates during summer 1999 (Fig. 2). Oviposition density (females m^{-2} day^{-1}) was used to compare oviposition rates between ponds, and was calculated using the estimates of oviposition rate and pond area (Caudill 2002).

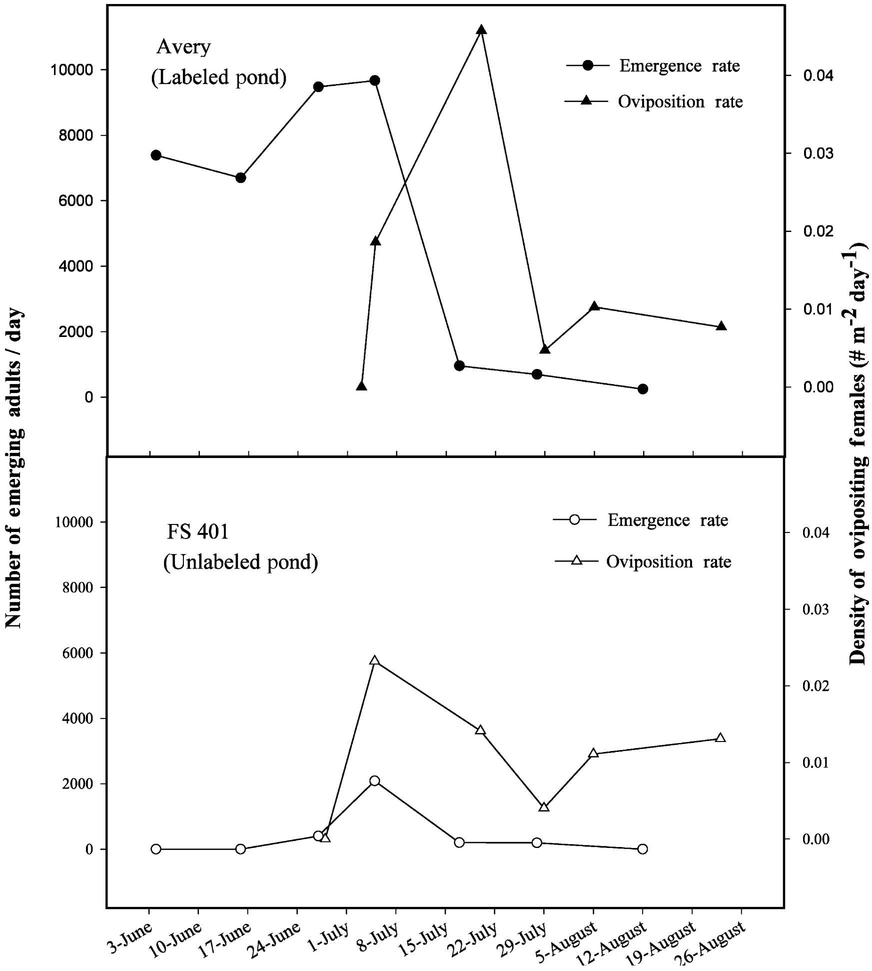
Males were collected from mating swarms from within 5 m of the margin of each pond on 9 July 1999. All mayflies were frozen until analysis. The isotopic composition of individual mayflies (δ^{15}N, expressed in parts per thousand, ‰) was determined using a PDZ Europa Hydra 20-20 mass spectrometer and a PDZ Europa ANCA-GSL elemental analyzer at the University of California Davis Stable Isotope Facility. Average analytical error, estimated as the S.D. of the isotopic ratio of an internal standard, was 0.17‰ ($n = 34$). Higher δ^{15}N values indicate greater uptake of the ^{15}N label.

Data analysis

Individual mayflies were qualitatively classified as marked or unmarked using a natural break in the distribution of δ^{15}N values obtained from adults, and these were compared to the isotopic ratios of larvae collected from the labeled pond before and after the ^{15}N addition (Fig. 3). A value of $\delta^{15}\text{N} \geq 5.0‰$ was chosen as the minimum labeled value for adults; the maximum value of individuals classified as unlabeled was 4.67‰ and the minimum of those classified as labeled was 5.73‰. Reclassifying two individuals with $\delta^{15}\text{N} = 4.5–5.0‰$ as labeled did not qualitatively affect the results. Naturally enriched individuals arriving from ponds outside the study system could not be recognized using this criterion, though individuals with natural $\delta^{15}\text{N} > 5.0‰$ were probably rare (Peterson 1999). In mayflies, the isotopic composition of larvae should accurately reflect that of adults because the adults do not feed (Edmunds et al. 1976), and there is little potential for changes in isotopic composition between molts (Hershey et al. 1993).

Two hypotheses concerning patterns of dispersal were tested using chi-square tests. First, frequencies of marked and unmarked individuals were compared between ponds within each sex. If the mayflies emerged into a completely mixed, regional population of adults, the frequency of marked individuals collected at each pond would be equal, irrespective of any differences in the population sizes of adults emerging from each pond. A Mantel-Haenszel chi-square test was used for the female data, which provided an overall test for differences in frequency of marked and unmarked females by comparing frequencies within each sampling date. A second analysis tested for potential differences in dispersal behavior between sexes by comparing the frequencies of marked and unmarked males and females within each pond. Monte Carlo simulations (Roff and Bentzen 1989) were used to perform a second chi-square test due to low frequency of unmarked individuals at the Avery pond. Frequencies of females were pooled across all dates for comparisons between sexes, and p-values were estimated using 10 000 iterations.

Fig. 2. Pattern of emergence and oviposition at the two study ponds. Emergence began at Avery before FS 401. The close overlap in emergence and oviposition at FS 401 suggested immigration from a phenologically advanced pond (e.g. Avery) because adult females incubate fertilized eggs in the terrestrial habitat for two weeks between emergence and oviposition, yet few females had emerged from FS 401 two weeks before the peak oviposition at this pond.



Results

Emergence of *Callibaetis* adults from Avery Pond began approximately one month before emergence at FS 401 (Fig. 2). However, the peak emergence at FS 401 and Avery overlapped. Peak oviposition in Avery occurred approximately two weeks after peak emergence from both ponds, consistent with the expected delay due to the two-week egg incubation period for females. In contrast, the peaks of emergence and oviposition were concurrent at FS 401, providing indirect evidence of immigration from other ponds, because few females had emerged from FS 401 two weeks before the peak of oviposition.

Larvae in Avery assimilated ^{15}N within 2 weeks of the addition ($\delta^{15}N$ of last instar larvae collected on 3 June, the day of the first addition = 2.44 ± 0.200‰ S.D. (n = 3), 16 June $\delta^{15}N = 25.0 \pm 1.29$‰ (n = 2), 3 July $\delta^{15}N = 27.5 \pm 3.48$‰ (n = 2), 9 July $\delta^{15}N = 19.6 \pm 3.34$ (n = 2)). On the first date that ovipositing females were observed (5 July), all ovipositing females at Avery were marked (Fig. 4), consistent with the phenology of emergence from the two ponds on this date (Fig. 2). Females began emerging from Avery before larvae were labeled. However, the high $\delta^{15}N$ value in larvae sampled on 16 June, 3 weeks prior to the sampling of the first spent females (a period one week longer than the female terrestrial stage) suggests the sampled spent females originating from this pond were marked.

At the unlabeled FS 401 pond, 80% of the females collected were marked, demonstrating that most females had immigrated from Avery before ovipositing (Fig. 4). The proportion of marked females remained higher at Avery than FS 401 on subsequent dates, and the proportion marked at both ponds decreased throughout the emergence season. Overall, the frequencies of marked females at the two ponds differed (Mantel-Haenszel Chi-square = 11.251, 1 d.f., p = 0.001), with fewer marked females than expected at the unlabeled pond if adults recruited from a completely mixed regional pool of adults, suggesting some degree of isolation between ponds and/or immigration to this pond from other ponds in the metapopulation.

In contrast to the frequent movement between ponds by females, males were highly philopatric – a single

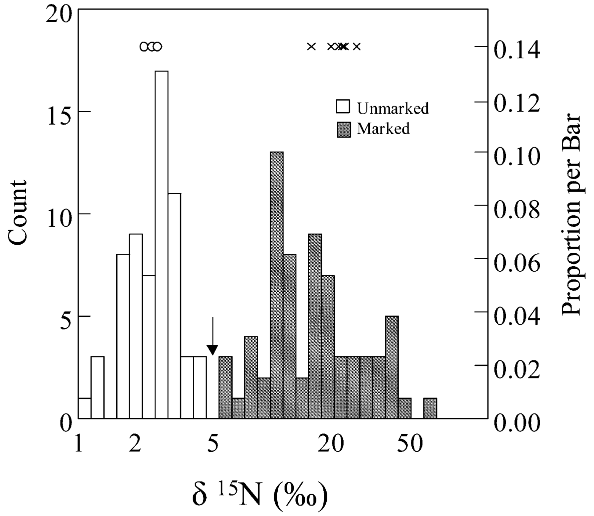


Fig. 3. Distribution of isotopic composition for all adult mayflies used in the study (bars) and larvae (symbols). Last instar larvae collected from the labeled pond 13–36 days after the addition ("x", $n = 6$) were enriched compared to those collected before the addition ("o", $n = 3$). The arrow denotes the minimum value used to classify individuals as marked ($\delta^{15}N = 5.0$‰; natural log scale used for clarity).

marked male was observed at FS 401 and no unmarked immigrants were observed at Avery (Fig. 5, Pearson chi-square = 36.190, 1 d.f., $p < 0.0005$). Within both ponds, the frequencies of marked and unmarked females and males differed, demonstrating sex-biased dispersal (Monte Carlo Chi-square simulations, FS 401 $p = 0.0017$; Avery $p = 0.0046$).

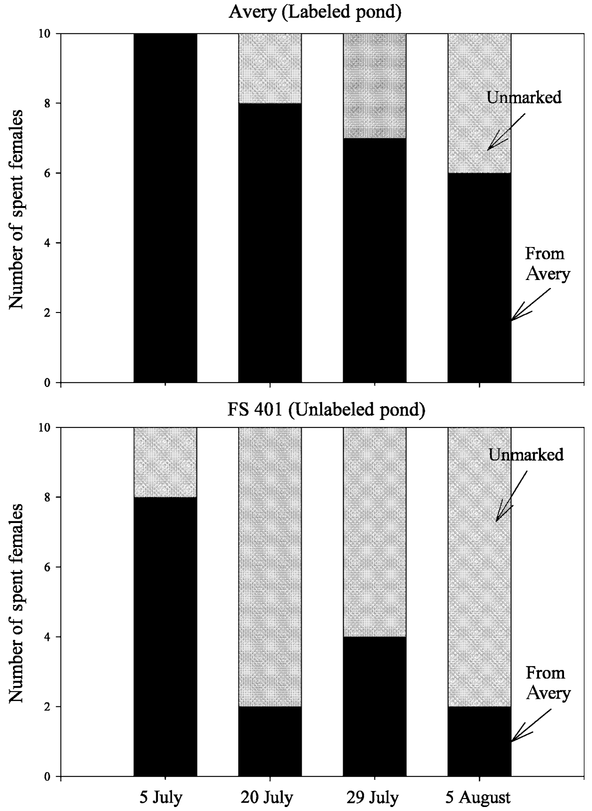


Fig. 4. The number of marked and unmarked spent females collected after they oviposited and died on the pond surface in the labeled and unlabeled pond during the experiment. Marked females from Avery flew to FS 401 and unmarked females flew from FS 401 or other unlabeled ponds to Avery before oviposition. The frequency of marked and unmarked females differed between ponds (Mantel-Haenszel Chi-square = 11.251, 1 d.f., $p = 0.001$).

Discussion

The results clearly demonstrate female dispersal between habitat patches (ponds) between emergence and oviposition. This movement represents natal or effective dispersal (Greenwood 1980), which should closely reflect potential gene flow since females were sampled after mating and completing all dispersal. More important in the context of this study, the dispersing females had a strong potential to affect local population dynamics (Caudill 2002, 2003). The movement by females among patches was a central feature of the source-sink dynamic observed in this metapopulation. Source-sink dynamics arise when individuals disperse among patches that differ strongly in habitat quality, but cannot select the patch that maximizes fitness (e.g. dispersal is constrained; Pulliam 1988, Dias 1996). During the study, many females from the marked pond, a demographic source during the study without fish, oviposited in FS 401, a trout pond that had a local population growth rate below replacement (Caudill 2002). In addition, oviposition rates did not differ between ponds with and without trout for twelve ponds in the metapopulation, demonstrating that females did not strongly avoid ponds with trout (Caudill 2003). In the previous generation of *C. f. hageni*, indirect data strongly suggested net migration from fishless ponds to ponds with trout (Caudill 2002); unfortunately, the net direction of dispersal between Avery and FS 401 during 1999 could not be assessed with these data.

What mechanisms may constrain site selection by *Callibaetis* females? Since females do disperse among ponds, they may 'sample' multiple ponds before oviposition. However, this is unlikely given the short lifespan and limited metabolic resources of adults. Since adults do not feed (Edmunds et al. 1976), and daily adult mortality was higher than larval mortality (Caudill 2002), assessing the quality of, and selecting among, several ponds may be more costly to females than ovipositing in a pond of low quality for larval development. Further, mayflies appear to rely solely on visual cues to select oviposition sites, a sensory modality that is unlikely to provide reliable information signaling the presence of trout. Mayflies have been observed

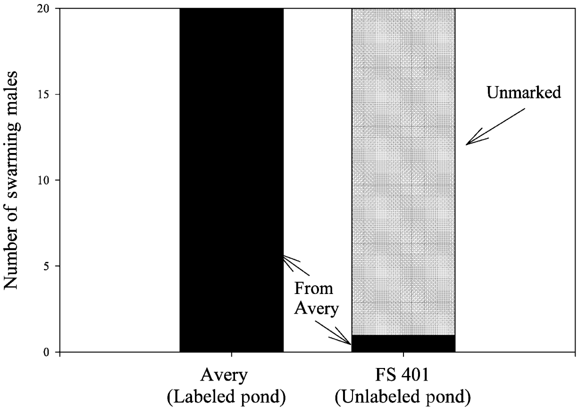


Fig. 5. Number of marked and unmarked adult males collected from mating swarms at the banks of the labeled Avery and unlabeled FS 401 ponds. The frequencies of marked and unmarked males differed between ponds (Pearson chi-square = 36.190, 1 d.f., $p < 0.0005$). Males were philopatric compared to females – only one single marked male was observed at the unlabeled pond, demonstrating female-biased dispersal at both ponds (Monte Carlo Chi-square simulations, FS 401 $p = 0.0017$; Avery $p = 0.0046$)

ovipositing on plastic sheeting, waste oil pools, cars, and dry asphalt in large numbers, apparently deceived by reflected polarized light (Kriska et al. 1998). Thus, high adult mortality and sensory limitation may constrain oviposition site selection by *Callibaetis*.

This study also provides strong evidence for female-biased natal dispersal (Fig. 4 and 5). Sex-biased dispersal occur in many groups including other insects (Roff 1990, Michiels and Dhondt 1991, Albrectsen and Nachman 2001, Srygley 2001), sharks (Pardini et al. 2001), birds and mammals (reviews by Greenwood 1980 and Clarke et al. 1997). The dispersing sex frequently differs among taxa, and a number of mechanisms have been proposed to explain intersexual differences in dispersal behavior including differences in sex chromosomes, phylogeny, ecological conditions, and mating systems (Greenwood 1980). Greenwood (1980) concluded that the mating system, specifically traits increasing access to more matings (for males), or resources, especially food, during the reproductive period (for females), best explained patterns of sex-biased dispersal. The pattern of sex-biased dispersal in *Callibaetis* correlates especially well with the mating system. Because nearly all male mayflies detect and mate with females while flying (Edmunds et al. 1976, Allan and Flecker 1989, Harker 1992), male mating success will be influenced in part by total searching time. Males fly using larval energy reserves and flight is energetically costly. Hence, by swarming at the emergence site rather than first dispersing, males will increase potential searching time. In addition, the pattern of female availability may contribute to the philopatry observed for male *Callibaetis ferrugineus hageni*. In most mayflies there is a spatial and temporal separation between emergence and mating because both males and females molt to the imago stage prior to copulation (Needham et al. 1935, Edmunds et al. 1976, Edmunds and McCafferty 1988). However, female *C. f. hageni* mate as subimagos immediately after emerging and within meters of their natal ponds, and the location of emergence represents a reliable location of sexually receptive females. Thus, dispersal by males could be costly for at least two reasons: movement would consume stored resources, and could take males away from a reliable source of potential mates.

In contrast to male philopatry, adult female mayflies are the primary dispersal and colonization stage of this taxon. Relatively long distance flight by females before oviposition may be common in mayflies (Flecker and Allan 1988, Hershey et al. 1993, Kureck and Fontes 1996). For instance, Kureck and Fontes (1996) reported that female *Ephoron virgo* (Ephemeroptera: Polymitarcyidae) did not land soon after mating and fertilized females were observed up to 20 km from the emergence site, whereas males were only found near the emergence site. Dispersal by females may be especially important for *Callibaetis* spp., which live in variable, and often ephemeral, environments (Edmunds et al. 1976, Wiggins et al. 1980, Wellborn et al. 1996). The ultimate selection pressures shaping adult female mayfly dispersal behavior remain unclear, but likely involve a trade-off between reproductive effort and historical selection for colonization ability.

Finally, sex-biased dispersal, if unrecognized, has the potential to compromise dispersal estimates. For example, strongly female-biased dispersal has been observed in other baetid mayflies (Flecker and Allan 1988). Hershey et al. (1993) estimated female dispersal in *Baetis* sp. adults using ^{15}N enrichment but did not determine the sexes of analyzed adults (Hershey et al. 1993, p. 2318). If *Baetis* sp. males were also philopatric, then the presence of males in their composite samples could have resulted in an underestimation of the true distances females dispersed, and could thereby compromise Hershey et al.'s (1993) conclusion that female upstream flight closely matches the distance dispersed downstream during larval stages.

The stable isotope enrichment technique used here has the potential to increase our understanding of dispersal in metapopulations and sexual differences in dispersal behavior, especially in taxa that are difficult to mark in large numbers by conventional means (Hagler and Jackson 2001). The semelparous mayflies used in this study were ideal because the stable isotope label incorporated by larvae was not 'diluted' by adult feeding. Nonetheless, the technique should be broadly applicable in taxa where elemental turnover is low in some body compartment during adulthood (e.g. chitin, wings), body size is not limiting, and sufficient enrichment can be achieved. While only one patch was marked in this experiment, the potential for marking multiple patches exists by using several elements singly or in combination. For example, all individuals in a four-patch metapopulation could be recognized using ^{13}C, ^{15}N, ^{13}C plus ^{15}N, and no enrichment. Studies of this type will be especially fruitful given the importance that the details of dispersal have in determining metapopulation dynamics (Travis and French 2000), and the current paucity of empirical data.

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