

Contradictory results from different methods for measuring direction of insect flight

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SUMMARY

1. Stream ecologists have been puzzled by the apparent paradox that invertebrate populations persist in headwater streams despite the high frequency with which individuals drift downstream. To resolve this 'drift paradox', directions and distances of both larval and adult movement must be identified. Using over 50 interception traps in combination with results from several mark–capture experiments using ¹⁵N as a label, we tested the assumption that interception traps accurately represent the ultimate direction of adult insect flight.

2. In several streams in the Hubbard Brook Experimental Forest, 76% of ¹⁵N-labelled stoneflies (*Leuctra ferruginea*) had flown upstream from where they emerged to where they were captured. In contrast, over 60% of stoneflies were flying downstream when captured, i.e. on the upstream side of an interception trap.

3. The instantaneous direction, as indicated by the side of the interception trap on which they were captured, indicated the ultimate flight direction for fewer than 1/3 of the individuals captured. Thus, such traps did not accurately reflect the ultimate flight patterns of individuals, as indicated by mark–capture data.

4. Conclusions drawn from interception trap counts regarding the direction of movement and the distribution and persistence of populations may need to be re-evaluated. We suggest that better tracking methods, including mass mark–capture studies using stable isotopes, be used to evaluate the potentially complex patterns of adult insect movement and the consequences of that movement for individuals and populations.

Keywords: aquatic insects, colonisation cycle, flight direction, mark–recapture, stonefly

Introduction

The observation that populations of aquatic invertebrates persist in headwater streams despite the high frequency with which they are found in the drift has perplexed aquatic ecologists and entomologists for over 70 years (Muller, 1954; Waters, 1961, 1965; Mostram cited by Muller, 1982; Hershey *et al.*, 1993; Williams & Williams, 1993; Anholt, 1995; Winterbourn & Crowe, 2001; Petersen *et al.*, in press). This apparent

'drift paradox' (Hershey *et al.*, 1993; Anholt, 1995) has generated considerable empirical and theoretical research relating to the dispersal of individuals and its consequences for populations. In his 'colonisation cycle' hypothesis, Muller (1954, 1982) proposed that upstream flight is necessary to compensate for the net displacement of individuals downstream. Alternatively, Waters (1961, 1965) proposed that because 'drift removed only those organisms produced in excess of the stream bottom capacity', random flight by those remaining upstream would be sufficient for maintaining upstream populations. Others have similarly concluded from mathematical models that random flight may be sufficient for persistence of headwater

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populations (Anholt, 1995; Speirs & Gurney, 2001); yet upstream dispersers drive random dispersers to extinction in some simulations (Anholt, 1995). Thus, for evaluating alternative hypotheses regarding flight direction and its consequences for populations, it is critical to know the directions and distances moved by adults and larvae.

Most studies describing flight direction have relied on counts from one or several traps that intercept insects as they fly along streams. Such interception traps include hanging sticky traps (Madsen, Bengtson & Butz, 1973; Neves, 1979; Bird & Hynes, 1981; Flecker & Allan, 1988; Winterbourn & Crowe, 2001), Malaise traps (Mendl & Muller, 1979; Jones & Resh, 1988; Williams & Williams, 1993; Petersen *et al.*, 1999), window traps (Muller, 1973; Svensson, 1974; Mendl & Muller, 1979), or any trap that is oriented with two or more sides available for collections.

One common assumption of these methods is that the direction of flight is indicated by the side on which the insect is caught. A second assumption is that the direction of flight at the moment of capture accurately reflects large-scale movement (Muller, 1954, 1973, 1982; Madsen *et al.*, 1973; Mendl & Muller, 1979; Neves, 1979; Flecker & Allan, 1988; Petersen *et al.*, 1999; Winterbourn & Crowe, 2001). Specifically, if the majority of individuals were caught on the downstream sides of traps, researchers have generally concluded that females were flying, and consequently ovipositing, upstream from where they had emerged; such data support the 'colonisation cycle' hypothesis. Likewise, if equal numbers of individuals were caught on both sides of a trap, it has often been concluded that the flight pattern was non-directional or random, and thus that the behaviour of that species did not conform to the colonisation cycle (Bird & Hynes, 1981; Jones & Resh, 1988; Williams & Williams, 1993; Petersen *et al.*, 1999).

In this paper we compare results from several mark-capture studies to concurrent data from interception traps to evaluate conclusions about dispersal direction and the 'colonisation cycle'. While it may be questioned whether trap counts reflect active flight behaviour or passive transport via wind, there is no doubt that individuals caught on one side of a trap were moving in that direction at the moment of capture (instantaneous flight direction). In this study we test the assumption that the instantaneous flight

direction of an individual is representative of its net direction from the point of emergence (ultimate flight direction). We argue that, without such a test, conclusions based on interception trap data regarding the consequences of perceived directional flight on population dynamics may be premature.

In four experiments in streams within the Hubbard Brook Experimental Forest (HBEF), NH, U.S.A. we used an isotopic tracer, ^{15}N , to identify the ultimate flight direction of individual stoneflies, and the approximate distance travelled, from labelled sections of streams to their sites of capture (Macneale, 2003). Here, we describe this mass mark-capture technique and results using this method, and compare those data with collections of stoneflies on interception traps hanging across streams. We asked two questions: (i) What was the probability that a labelled individual caught on the downstream side of a trap had emerged from a location downstream of that trap (i.e. was it dispersing upstream)? (ii) Can the relative counts of individuals caught on the up- and downstream sides of traps be used to predict the overall direction of dispersal of a population? In this case, the numbers captured on each side of a trap should reflect the same patterns of ultimate flight direction that we obtained from the mark-capture data.

Methods

We examined adult dispersal of an abundant stonefly, *Leuctra ferruginea* (Walker) (Insecta; Plecoptera; Leuctridae), within the HBEF, North Woodstock, NH, U.S.A. (lat. 43°56'N, long. 71°45'W). The nymphs feed on detritus in small, cold headwater streams throughout northeastern North America. Seven *Leuctra* species, distinguishable only as adults, inhabit first and second order streams in the HBEF (Fiance, 1977; Macneale, 2003). The nymphal density of *Leuctra* spp. is typically approximately 1000 m⁻² (Hall, Likens & Malcom, 2001), and drift rate is low (2.4 ± 0.9 individuals 100 m⁻³, Macneale, 2003). Adult *L. ferruginea* emerge from mid July until late August (approximately 200 m⁻²), and females live 4–8 weeks as adults. Females must feed extensively to develop eggs in the adult stage, and therefore do not begin ovipositing until at least 2 weeks after emergence (Macneale, Likens & Peckarsky, 2002; Macneale, 2003).

Estimating dispersal distance and direction from ^{15}N additions

To estimate the distance and direction flown by adult *L. ferruginea*, we trapped individuals emerging from streams that had been 'labelled' with ^{15}N , an isotopic tracer. In four experiments, $^{15}\text{NH}_4\text{Cl}$ (10% ^{15}N) was added to three streams in HBEF (Table 1), to enrich isotopically (label) the detrital food of stonefly nymphs and ultimately the adults emerging from those stream reaches. The degree ($\delta^{15}\text{N}$ of individual stoneflies) and extent of enrichment (m^2 of stream) were determined by analysing the $\delta^{15}\text{N}$ value of individual adult *L. ferruginea* emerging from up to 11 sites downstream of the point of each addition (i.e. 0 m in Fig. 1) throughout the entire *L. ferruginea* emergence period. The $\delta^{15}\text{N}$ values of potentially labelled individuals were compared with reference (non-labelled) *L. ferruginea* emerging at least 25 m upstream of each addition site. A freshly emerged *L. ferruginea* was considered labelled when its $\delta^{15}\text{N}$ value was greater than a conservative threshold defined as two standard deviations above the mean $\delta^{15}\text{N}$ value of the reference *L. ferruginea*. For example, the mean $\delta^{15}\text{N}$ value for reference individuals was 3.02‰, and the conservative threshold (± 2 SD) was 4.25‰, above which we considered individuals from Zig Zag Brook to be labelled (Macneale, 2003).

While a female emerging with a $\delta^{15}\text{N}$ value 4.5‰ may have been enriched relative to non-labelled individuals, she did not retain a sufficient amount of that ^{15}N after feeding as an adult to be detected as labelled. We discovered that, because of feeding extensively on terrestrial food sources, unlabelled females depleted their $\delta^{15}\text{N}$ value by approximately

2‰ by the time oviposition began (Macneale, 2003). Using a mixing model to determine the depletion of $\delta^{15}\text{N}$ in labelled females, we determined that females emerging with $\delta^{15}\text{N}$ values of $<7\%$ would effectively 'lose' their label before returning to the stream (Macneale, 2003). Accordingly, we adjusted the threshold for determining whether or not mature females were labelled to account for adult feeding and to include only those that had emerged with $\delta^{15}\text{N}$ values of $>7\%$ (Macneale, 2003). Individual stoneflies were analysed using a Europa Scientific Geo 20/20 at the Cornell Laboratory for Stable Isotope Analysis, or a Europa Scientific Hydra 20/20 at the Stable Isotope Facility at the University of California, Davis; blind standards analysed with each set of samples at each lab showed $\delta^{15}\text{N}$ precision was consistently within $\pm 0.2\%$.

To estimate the flight direction and distance of adult stoneflies, we collected flying stoneflies as well as stoneflies resting on vegetation, using sweep nets and, in some years, interception traps placed upstream, within and downstream of labelled stream reaches. Except for collections made early in the flight period in 1997 to assess flight behaviour of freshly emerged individuals including immature females (those without fully developed eggs) and males, we focused our analyses for each stream on mature female stoneflies (those with fully developed eggs) caught during the peak oviposition period.

The ^{15}N -label enabled us to determine the minimal distance and 'ultimate direction' of flight for individual stoneflies (the net direction travelled from the estimated site of emergence to the capture site). For stoneflies caught and found to be labelled, the minimum linear distance travelled by each

Table 1 Details of $^{15}\text{NH}_4\text{Cl}$ additions to three streams in the Hubbard Brook Experimental Forest, NH

Stream site	Start date of enrichment	Length of ^{15}N addition (days)	Target enrichment of streamwater NH_4 (‰)	Mean (SE) discharge during enrichment ($\text{m}^3 \text{day}^{-1}$)	^{15}N added during enrichment (mg)	<i>L. ferruginea</i> that emerged labelled (approximate no.)
Bear Brook ^{*†}	17 June 1997	42	500	2592 (967)	190	50 000
Bear Brook [†]	6 July 1998	30	1000	1229 (205)	98	250 000
Cascade Brook [‡]	3 June 1999	41	1000	676 (256)	57	19 000
Zig Zag Brook [‡]	24 May 2000	56	1500	776 (142)	171	112 000

The number of *Leuctra ferruginea* that emerged labelled was estimated for each addition by multiplying the mean number emerging (m^{-2} , see Macneale, 2003) and the area of stream that was enriched (m^2).

^{*}This addition was part of the LINX project (Peterson *et al.*, 2001).

[†] $^{15}\text{NH}_4\text{Cl}$ was dripped at a constant rate regardless of stream discharge.

[‡]the drip rate of $^{15}\text{NH}_4\text{Cl}$ was adjusted daily to match discharge.

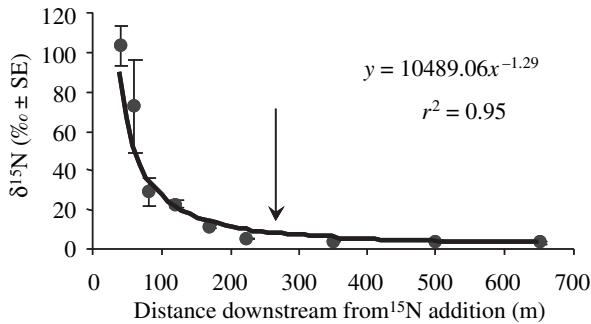


Fig. 1 The mean (\pm SE) $\delta^{15}\text{N}$ -values (‰) of emerging stoneflies at nine emergence sites along Zig Zag Brook ($n_{\text{total}} = 95$). The arrow indicates the effective endpoint of the labelled section. Similar patterns were found in all streams (Macneale, 2003). Regression equation is given for exponential decay function.

stonefly was calculated as the difference between the estimated site of emergence and the known site of capture. Given that we could not precisely estimate the site of emergence of each individual, we assumed that all labelled individuals had emerged from the midpoint of the labelled stream section. We defined the upstream endpoint of the labelled section as the upper-most site where labelled individuals emerged, the downstream endpoint where the mean $\delta^{15}\text{N}$ value of emerging stoneflies was approximately 7‰ (see above and see vertical arrow in Fig. 1).

Estimating dispersal direction from interception traps

During two of the ^{15}N additions, we collected stoneflies on traps hanging across streams (1997 along Bear Brook and 2000 along Zig Zag Brook). We use the term 'instantaneous direction' to refer to the direction an individual was flying the instant it was caught in an interception trap. For example, if caught on the upstream side of a trap, the instantaneous flight direction would be downstream.

On Bear Brook, we used 22 non-sticky traps that were distributed within 500 m up- and downstream of the ^{15}N -addition site. These traps consisted of a 1×1 -m piece of fibreglass mesh window screen suspended with the top of the trap approximately 1.5 m above the water surface. An individual found resting on a screen was collected by gently coaxing it to crawl into a glass vial. This collection method did not disturb other stoneflies resting on the screen, enabling collection of all individuals from

both sides. The mesh size was sufficiently small (<2 mm) that no individuals could crawl through the screen to change sides. Screens were checked and collections made one to three times per day for 14 days. Because these screens were not sticky, the number of stoneflies caught on each side represents those present at the time of collection only. While it is conceivable that individuals could crawl around these traps, individuals were remarkably stationary. We observed an occasional individual crawling straight up the trap surface, but never observed any crawling down, horizontally or towards or around an edge.

Along Zig Zag Brook in 2000, we collected mature females from sticky traps positioned every 50 m for 500 m upstream and 1000 m downstream of the ^{15}N -addition site. Sticky traps consisted of smaller (35×35 -cm) square screens coated thinly with Tangle-TrapTM adhesive (The Tanglefoot Company, Grand Rapids, MI, U.S.A.). At least two traps were positioned per site, each suspended with the top of the trap approximately 1.5 m above the stream. All stoneflies were collected from the traps every 2–3 days for the entire flight period (mid-July to October).

Statistical analysis

By comparing both methods for each individual we were able to determine whether its 'instantaneous direction', obtained from an interception trap, was a good indicator of its net ultimate flight direction obtained from the mark–capture data. Instantaneous direction data were analysed using a paired *t*-test for counts on sides of individual traps. We assumed sticky and non-sticky traps were equally effective at recording the instantaneous direction of flight because individuals moved very little when observed on non-sticky traps (and were not able to move at all when on sticky traps). In addition, we determined the proportion of individuals whose ultimate direction of flight was predicted accurately by their instantaneous flight direction. Using labelled individuals captured on each side of traps upstream of labelled stream sections, we determined the proportion of those actually caught while flying upstream. If the instantaneous directions were accurate, we would expect that 100% of the labelled individuals caught upstream of the labelled sections would also be caught while flying upstream.

Stream, year, sex and age of <i>L. ferruginea</i>	Mean distance (m)		Distance (m)	
	Upstream	Downstream	Upstream	Downstream
Bear Brook 1997				
Males	179 (44, 15)	170 (<i>n</i> = 1)	730	170
Immature females	179 (26, 20)	170 (100, 2)	530	270
Mature females	355 (<i>N</i> = 1)	NA	355	NA
Bear Brook 1998				
Mature females	234 (25, 23)	71 (23, 4)	479	121
Cascade Brook 1999				
Mature females	194 (34, 6)	45 (25, 2)	330	70
Zig Zag Brook 2000				
Mature females	219 (13, 80)	162 (14, 36)	663	287
All streams combined	211 (10, 145)	149 (13, 45)	730	287

Table 2 Minimal net distances dispersed by *Leuctra ferruginea*

Individuals are grouped by stream, year, sex, stage and whether their ultimate flight direction was upstream or downstream from their estimated site of emergence. Standard errors and sample sizes, respectively, are given in parentheses.

Results

Distance and direction of dispersal estimated from ¹⁵N data

The mean (\pm SE) distance flown by individuals from their emergence sites to where they were captured along the stream was 197 (\pm 9) m (*n* = 190). Of these individuals, 76% had flown upstream distances ranging from 1 to 730 m (Table 2). The proportion of labelled individuals caught upstream of labelled sections often approached or exceeded 50% (for example Zig Zag Brook, Fig. 2), further illustrating that large numbers of adults ultimately moved upstream over their adult lives.

Comparison of results using the two different methods

Our most striking finding was the discrepancy between the ultimate directions (obtained from mark–capture data, Table 2; Fig. 2) and the instantaneous directions (obtained from trap data, Figs 3 & 4). The ultimate direction dispersed was upstream for 76% of *L. ferruginea* adults (Table 2). Moreover, the proportion dispersing upstream and the mean distances dispersed did not differ among males, immature females or mature females (Table 2; Fig. 2). The instantaneous direction, however, was upstream for only 40% of mature females (i.e. only 40% were flying upstream when they were captured, Fig. 3). In addition, fewer than half the mature females caught upstream of where they had emerged were caught while flying upstream (Table 3). The most extreme case was one female caught

on the upstream side of a trap approximately 663 m upstream from her emergence site.

This discrepancy between results using the two methods was even more pronounced for *L. ferruginea* males and immature females. While >75% of males and immature females were captured upstream of the sites where they emerged (Table 2), the instantaneous direction of flight was upstream for only 23% of males and 17% of immature females collected on Bear Brook (Fig. 4). Data for all dates are combined in Fig. 4 but the pattern is consistent if analysed by trap or by day. In addition, the probability of catching a labelled male or immature female upstream of the addition site was much greater on the upstream side of the traps, although each had ultimately flown upstream (Table 3).

Discussion

The number of *L. ferruginea* caught on either side of hanging traps did not accurately indicate the direction individuals were ultimately dispersing from their site of emergence. In fact, results from this study suggest that the instantaneous flight direction may even predict the opposite pattern of flight known from mark–capture experiments. While most individuals were caught on both sticky and non-sticky traps while flying in a downstream direction, the majority of individuals were caught upstream from their emergence site. Therefore, it may be inappropriate to use interception traps to assess the ultimate direction of flight for *L. ferruginea* in the HBEF streams.

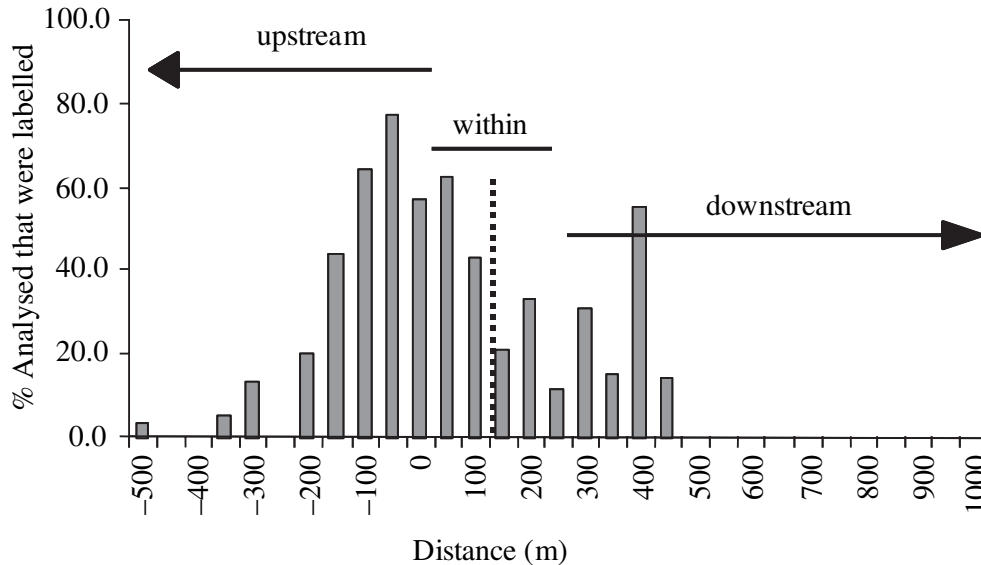


Fig. 2 The proportion of analysed mature females that were ¹⁵N-labelled at each site along Zig Zag Brook. Arrows indicate sites upstream, within and downstream from the ¹⁵N addition site (0 m) on Zig Zag Brook. Approximately 20 females were analysed from each site (one site every 50 m, $n_{\text{total sites}} = 31$, $n_{\text{total individuals}} = 619$); note that no labelled females were found at three upstream and 11 downstream sites. Vertical dotted line indicates estimated midpoint of labelled reach.

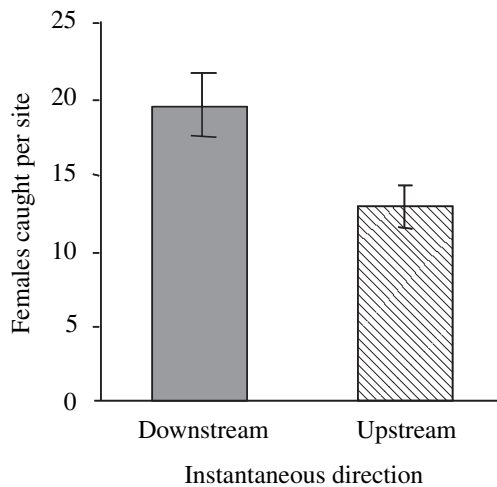


Fig. 3 The mean (\pm SE) number of mature female *L. ferruginea* caught per site while flying downstream or upstream at Zig Zag Brook, during the peak oviposition period (12–26 September 2000). Collections include all individuals for which we had recorded the side of the trap on which they were collected; $n = 26$ sites, 850 individuals, t -ratio = 4.49, $P < 0.0001$.

The consistent pattern of greater numbers caught while flying downstream, regardless of stream, trap location, trap stickiness or day, suggests that abiotic factors that vary by site and by day (e.g. wind direction, temperature, humidity) may have little

effect on the direction of instantaneous movements of *L. ferruginea* adults in the HBEF streams. Although no individuals were observed flying during rain or at night, we did observe individuals flying during all daylight hours and shortly before and after rainfall events. While Bear Brook flows in a south-easterly direction, and therefore downstream flight could be affected by the prevailing northwest winds (<http://www.hubbardbrook.org>), we observed similar flight patterns and trap collections along Zig Zag Brook, which flows primarily north. Finally, if the direction of the prevailing wind affected flight direction, we would expect that instantaneous flight direction would be a better predictor of ultimate flight direction. Because most interception traps collect individuals passively while they are flying within a few metres above the stream or ground, we assume our results from sticky and non-sticky traps would be representative of patterns found using other interception traps (i.e. Malaise traps).

The data presented here suggest that interception traps may be appropriate for assessing the instantaneous flight direction of individuals while they are flying a few metres above the stream surface. Our observations of live, flying individuals corroborate the patterns observed on traps: the majority of individuals observed flying near the stream surface

Table 3 The accuracy of interception traps in determining ultimate flight direction. Trap accuracy is the percentage of individuals ultimately caught flying upstream that were also caught while flying upstream. Traps on Zig Zag Brook and Bear Brook were sticky and non-sticky, respectively.

Age and sex of <i>Leuctra ferruginea</i> and site	Total number of labelled stoneflies caught upstream of ^{15}N addition sites (ultimate direction = upstream)	Number of labelled stoneflies captured while flying upstream (instantaneous direction = upstream)	Trap accuracy (%)
Mature females, Zig Zag Brook	49	22	44
Immature females, Bear Brook	20	1	5
Males, Bear Brook	15	3	20
All individuals, all streams	84	26	31

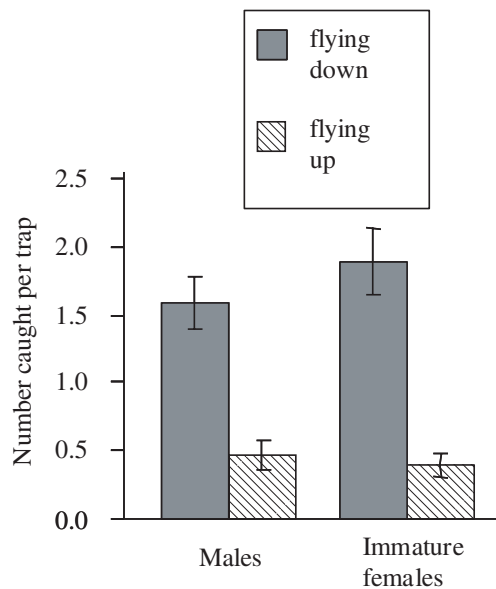


Fig. 4 The mean (\pm SE) number of *L. ferruginea* males and immature females caught per trap while flying downstream or upstream at Bear Brook, 5–11 August 1997. Analyses include all individuals collected each time traps were checked when there was at least one individual on either side of a trap; $n = 69$ trap checks (138 sides); males: t -ratio = 5.07, $P < 0.0001$; immature females: t -ratio = 5.78, $P < 0.0001$.

were heading downstream. This instantaneous snapshot may reveal important behaviour (e.g. female search pattern for suitable oviposition habitat at a local scale). Counts from interception traps may also be appropriate for assessing the relative density of adults across sites (e.g. among streams). However, given our findings, one cannot assume that trap counts alone indicate the ultimate direction of dispersal from the site of emergence. Consequently, methods that measure ultimate flight (and not instantaneous flight) must be used to evaluate the

biological significance of the 'colonisation cycle' model, which predicts that upstream populations persist because of predominantly upstream recruitment by ovipositing females.

One possible explanation for the discrepancy between these two methods for identifying flight direction is that the ultimate upstream movement calculated using the mark-capture technique occurs in space other than a few metres above the stream. We have observed that males and females of a closely related species, *Leuctra tenella* (Provancher), are distributed fairly evenly throughout the lower half of the forest canopy (Macneale, 2003). Therefore, we suspect that individuals may disperse upstream while they are more than a few metres vertically and/or laterally from the stream surface (Macneale, 2003).

Whether trap counts can indicate ultimate flight directions accurately for other species depends on the species and its behaviour. For example, species with short-lived adults (e.g. most mayflies) presumably fly less often and/or for shorter distances than *L. ferruginea*; thus flight immediately above the stream may in fact represent their ultimate flight direction. However, many species with short-lived adults have complex adult behaviours relating to finding mates and selecting oviposition sites (Stewart, 1994; Peckarsky, Taylor & Caudill, 2000; Peckarsky *et al.*, 2002). *Baetis* mayflies, for example, form swarms that can occur far from streams, and females search for and select specific rocks under which they oviposit (Peckarsky *et al.*, 2000, 2002). Such behaviour could involve multidirectional flights after a unidirectional or simply vertical dispersal event. Jackson & Resh (1989) found that the adults of three of 12 common taxa of stream insects were found in highest densities 8 m above the stream on sticky traps distributed up to 8 m in the canopy (trees were 10–20 m tall), and only

one taxon was most abundant 2 m above the stream. Therefore, the optimal roosting location or swarming site may be upstream, downstream, or near the site of emergence (at varying heights in the surrounding vegetation), and the optimal oviposition site may be upstream or downstream from there. In addition, movement patterns of feeding adults may be very different from movements involved in mate searching or selecting oviposition sites.

Many biotic and abiotic factors have been shown to affect adult insect flight, including light, temperature, humidity and wind, the distribution and structure of riparian vegetation, the distribution of mates and preferred mating sites, and the distribution of food resources (Jackson & Resh, 1989, 1991; Zwick, 1990; Stewart, 1994; Collier & Smith, 2000; Smith & Collier, 2000; Briers, Cariss & Gee, 2002, 2003). Consequently, for other species, as with *L. ferruginea*, a snapshot of individual behaviour may only be useful to determine in what direction it was moving at a particular height above the stream at one instant. Importantly, increasing the sample size of interception traps did not provide a more accurate picture of ultimate movements.

We conclude that to quantify ultimate flight direction and to speculate on the effects of directional flight on the distribution and abundance of *L. ferruginea*, data from mark-capture studies are necessary, while data from interception traps may be misleading. Whereas mark-capture studies are often more expensive and time consuming than studies using interception traps, instantaneous flight directions as recorded with interception traps are not representative of ultimate flight directions as indicated by mark-capture methods. As methods for tracking movement are evaluated, improved and compared, it will be possible to improve and refine our understanding of how dispersal affects the distribution and abundance of populations.

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