Distribution and dispersal of adult stream insects in a heterogeneous montane environment

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With 4 figures and 4 tables

Abstract: The distribution and dispersal of adult mayflies, stoneflies and caddisflies were investigated in an approximately 5 ha area of montane forest and grassland-scrub in the South Island, New Zealand. Low-flying insects were collected in 28 Malaise traps set along stream channels, in dry valleys and on hillsides for 8 weeks in late summer. Adult assemblages differed in forest and grassland and along valleys depending on distance from streams that were their probable sources. Stoneflies and mayflies occurred predominantly in forest and were taken mainly above the stream or very close to it. In contrast, caddisfly species exhibited a wide range of distribution patterns with some restricted to forest and others being found in both forest and grassland up to 300 m from the nearest likely source. Many females of several species that were taken well away from their natal stream (e. g., *Pycnocentria evecta* and *Aoteapsyche colonica*), were not fully developed, reproductively, suggesting they were dispersing inland to mature, whereas others packed with eggs (e. g., most *Hydrobiosis parumbripennis*) were more likely to be searching for oviposition sites. Many more male and female caddisflies were trapped in valleys than on hillsides, even where surface-water was absent, suggesting that valleys provide important corridors for dispersal, at least of low-flying individuals.

Key words: Stream insects, dispersal, Trichoptera, Plecoptera, Ephemeroptera, Malaise traps, New Zealand.

Introduction

The terrestrial adults of aquatic insects use flight to circumvent physical barriers, and to colonize new or previously disturbed habitats such as those scoured and denuded by spates (Smock 1996, Briers et al. 2003). Some adults also fly in search of food, mates or oviposition sites. The females of some caddisfly species may fly many kilometres inland to rest while their eggs mature (Ross 1944, Kovats et al. 1996), whereas non-mating flights of males are likely to be associated with more general dispersal or feeding (Jackson & Resh 1989). Feeding (and by implication flight away from streams) is also likely to be critical for egg production and development in at least some stoneflies as shown by MacNeale et al. (2002) in a study of *Leuctra ferruginea.*

Despite its prevalence and importance in the life histories of many aquatic species, dispersal of freshwater taxa, including insects is difficult to study directly, and dispersal events that are biologically important may remain undetected (Bilton et al. 2001). Nevertheless, Caudill (2003) was able to demonstrate movement of adult mayflies (*Callibaetis ferrugineus hageni*) between two beaver ponds 250 m apart by marking those in one pond with the stable isotope

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[15]N. Similarly, Hershey et al. (1993) calculated the frequency and distances traveled along a river by *Baetis* adults (Ephemeroptera) marked with ^{15}N, and two studies of ^{15}N-marked stoneflies (*Leuctra* spp.) showed that some flew up to 1 km from their natal stream into adjacent catchments (Briers et al. 2004, MacNeale et al. 2005).

Dispersal away from stream channels has also been estimated indirectly using intercept traps and light traps (Svennson 1974, Collier & Smith 1998), although, because light traps are attractants results obtained with them are not always easy to interpret (Sode & Wiberg-Larsen 1993). Malaise traps have been used most frequently to examine the lateral dispersal of Plecoptera and Trichoptera (e. g., Svennson 1974, Griffith et al. 1998, Petersen et al. 1999, Winterbourn 2005) although they are limited to catching insects flying within about 1 m of the ground. In their Malaise trap study Griffith et al. (1998) found that 16 of 17 common stonefly and caddisfly taxa decreased in abundance with distance from four streams and obtained maximum capture distances for the 16 taxa of 44–81 m. Collier & Smith (1998) found most adult caddisflies within 30 m of a forest stream, although a few were trapped up to 70 m away, and while some stoneflies collected by Briers et al. (2002) had flown hundreds of metres, 90 % were taken within 11 m of the stream channel. Similarly, Winterbourn (2005) found most adults of two abundant forest-dwelling notonemourid stoneflies very close to their natal stream, although occasional adults were taken in forest and adjacent grassland up to 40 m away. Despite their apparent rarity, the few adults that disperse greater distances are likely to play important ecological roles as colonizers of streams following disturbance. Furthermore, because they have the potential to exchange genetic material with adults from neighbouring populations (Svennson 1974, Collier & Smith 1998), they may modulate the action of selection and genetic drift in local populations (Slatkin 1985).

The aims of the present study were to investigate the distribution and dispersal of adult mayflies (Ephemeroptera), stoneflies (Plecoptera) and caddis (Trichoptera) (EPT species) within a heterogeneous landscape incorporating forest, grassland, hillside and valley in the South Island, New Zealand. Traps were set out to sample as diverse a range of conditions as possible, both along and at various distances and directions from Reservoir Bush Stream, which we assumed would be the primary source of insects.

Methods

Study area

The study was carried out at Cass, inland Canterbury (about 600 m a. s. l.) in the vicinity of the University of Canterbury field station (43° 02′ S, 171° 45′ E). Cass lies in a glaciated, inter-montane basin, which was extensively forested in pre-European times, but fire and grazing of stock have reduced the forest cover, substantially.

Malaise traps were set out in a roughly triangular area of about 5 ha on the southwest face of Cass Hill, which has a cover of short-tussock grassland and scrub, and some fragments of mountain beech forest (*Nothofagus solandri* var. *cliffortioides*). It is dissected by three small streams on its southern side. One of these streams, Reservoir Bush Stream, was in the centre of our study area and had an average discharge of about 2 L/s. Although its headwaters are in sub-alpine scrub, the stream passes through an approximately 2 ha patch of mountain beech forest in its middle reaches, before flowing through mixed tussock grassland and matagouri (*Discaria toumatu*)-dominated scrub to its confluence with Middle Bush Stream (Fig. 1). The latter stream arises east of Reservoir Bush and flows through a narrow valley prior to joining Reservoir Bush Stream at the foot of Cass Hill. Beyond the confluence of Reservoir and Middle Bush streams the valley opens out and the stream usually flows beneath the surface of a shingle fan before reaching Grasmere Stream. The latter is a productive lake outlet stream, and because it is the only other stream within 1.5 km of Reservoir Bush, is the likely source of many adult aquatic insects taken in the study. The forested sections of Reservoir Bush Stream and the adjacent Middle Bush Stream have EPT faunas dominated by leptophlebiid mayflies, *Deleatidium* spp., notonemourid stoneflies (*Spaniocerca zelandica* and *Cristaperla fimbria*) and a diverse fauna of caddisflies belonging to at least eight families of which Hydrobiosidae, Oeconesidae and Conoesucidae are most abundant (Friberg et al. 1997, Winterbourn & Crowe 2001). In the lower reaches of these two streams many of the same species are found (Ledger et al. 2002) and few EPT species appear to occur there and not in the forested reaches. In contrast, the fauna of Grasmere Stream includes other species of *Deleatidium*, no notonemourid stoneflies, and a very different assemblage of caddisflies dominated numerically by *Aoteapsyche colonica* (Hydropsychidae) and several species of Conoesucidae not found in Reservoir and Middle Bush streams (Death 1991). Furthermore, Oeconesidae are absent from Grasmere Stream and with the exception of *Hydrobiosis parumbripennis* and possibly some *Psilochorema* species whose larvae cannot be distinguished, its hydrobiosid fauna is distinct from those of the other two streams.

Over the course of the study, stream water temperature was monitored continuously in Reservoir Bush and above and below the confluence with loggers (Onset, Stowaway) and ranged from 6–15 °C; average about 11 °C. However, surface flow ceased about 50 m below the confluence and was also absent from Middle Bush Stream for about 100 m above the confluence. Air temperature and wind direction were not monitored.
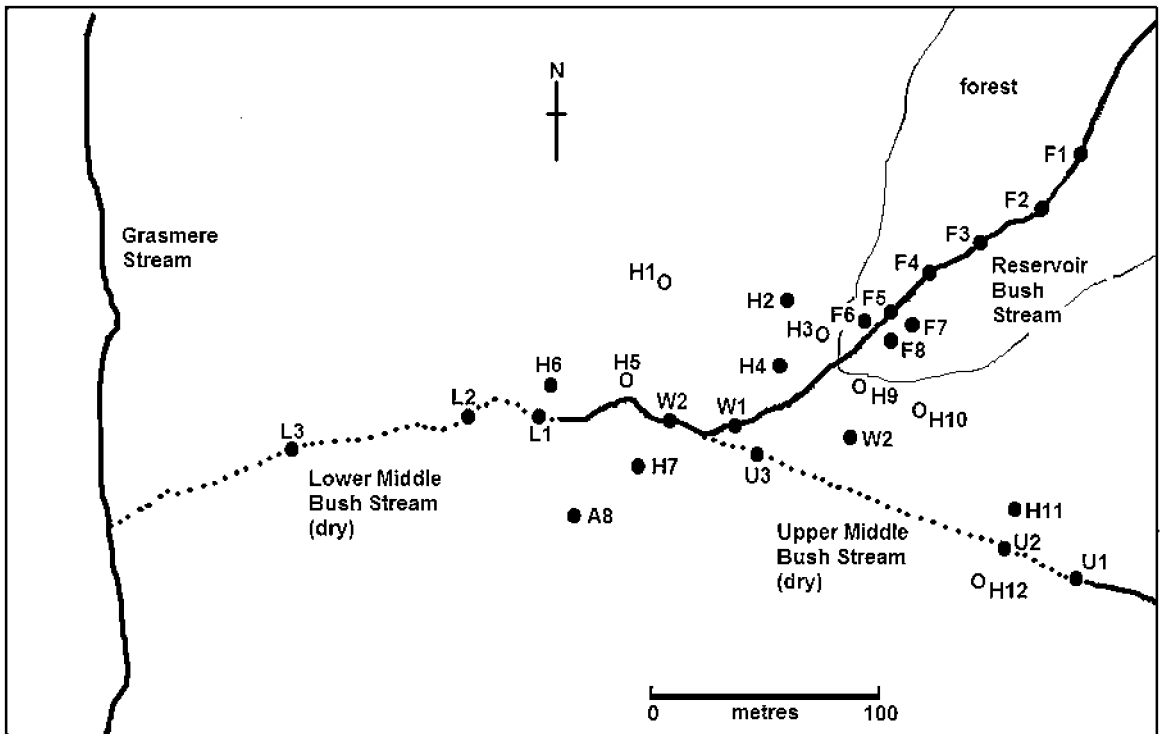
Fig. 1. Map of the Cass Hill area showing the distribution of the 28 Malaise traps and their proximity to Reservoir Bush, Middle Bush and Grasmere streams. Dotted lines indicate stream channels with no surface flow. Trap codes: forest (F), lower Reservoir Bush Stream (L), upper Middle Bush Stream (U), lower Middle Bush Stream (L), hillsides (H). Traps omitted from the ordination are shown as open circles.

Insect trapping

Adult stoneflies, mayflies and caddisflies were collected in 28 Malaise traps constructed from black or grey, 0.5 mm mesh shade cloth set up on Cass Hill and in associated stream valleys for 8 weeks during summer (late December – mid February) 2004–2005. Eight of the traps were in forest (Reservoir Bush), eight in the valleys below Reservoir Bush and Middle Bush, and 12 on the hillside outside the forest (Fig. 1). Thirteen of the traps were placed across the flowing stream (7) or its dry channel (6). All traps were oriented with the interception sheet (length 1.7 m, height 1.35 m, area 2.3 m^2) across the channel, or at right angles to the nearest stream. Insects entering the upstream and downstream sides of all traps (except F6, F7, F8 and H10 whose construction did not allow for their separation) were kept apart and preserved in separate jars of 95 % ethanol. Jars were emptied on 9 occasions between 3 January and 22 February 2005.

Sample processing and analysis

Adult mayflies, stoneflies and caddisflies (and mayfly subimagoes) were sorted from trap samples and identified to species level in most cases using the taxonomic works of Towns & Peters (1996), McLellan (1991, 1993) and Neboiss (1986) and a reference collection of caddisflies from Cass identified by John Ward (Canterbury Museum). All adults were sexed,

counted and stored in 70 % ethanol. As only the males of *Olinga feredayi* and *O. jeanae* can be distinguished morphologically (Ward & McKenzie 1997), females were identified to species by their distinctive stable nitrogen isotope (δ^{15}N) signatures (unpubl. data). These had a narrow range in both species (1.5 ppt) but were 5.2 times higher on average in *O. feredayi*, reflecting differences in the δ^{15}N values of foods eaten by larvae in their respective stream habitats.

The reproductive condition of female caddisflies belonging to five species (*Pycnocentria evecta*, *Olinga jeanae*, *Aoteapsyche colonica*, *Hydrobiosis parumbripennis*, *Edpercivalia fusca*) captured in 10 traps located in the upper (U1, U2, U3) and lower (L1, L2, L3, H6, H7) Middle Bush Stream valleys (Fig. 1) and at two forest sites (F2, F3) was assessed by dissection. Individuals were recorded as either (i) immature, (ii) maturing (with developing ovarioles and eggs), (iii) mature (with fully developed eggs), or (iv) spent (post-oviposition individuals with thin abdominal walls and no visible ovaries).

Insects captured on different dates were pooled to form a single data set, which was used for all analyses. Bray-Curtis polar ordination was used to search for patterns in the distribution of insects across sites (traps). It is a robust technique widely used in ecology for exploring the relationships of samples and species to environmental gradients (Gauch 1973, Wissinger et al. 2006) and was run using absolute abundance data in PC-ORD (McCune & Mefford 1999). The Sorensen distance measure and the variance-regression endpoint selection
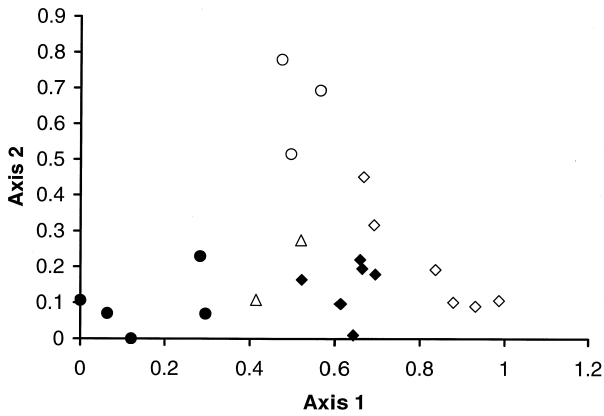
Fig. 2. Bray-Curtis ordination of insect assemblage data for 22 Malaise traps. Six traps that collected fewer than 6 individuals were omitted (see Fig. 1). Trap symbols: Reservoir Bush forest stream (●), riparian forest (○), lower Reservoir Bush Stream (△), upper Middle Bush stream valley (◆), lower Middle Bush stream valley (◇).

Fig. 3. Abundance of Ephemeroptera, Plecoptera and Trichoptera in Malaise traps within 3 landscape units, expressed as mean numbers (+ 1 SE)/trap.

method were used. Six traps that had captured < 6 individuals were omitted from the ordination analysis; all were in grassland away from wet or dry stream channels (Fig. 1).
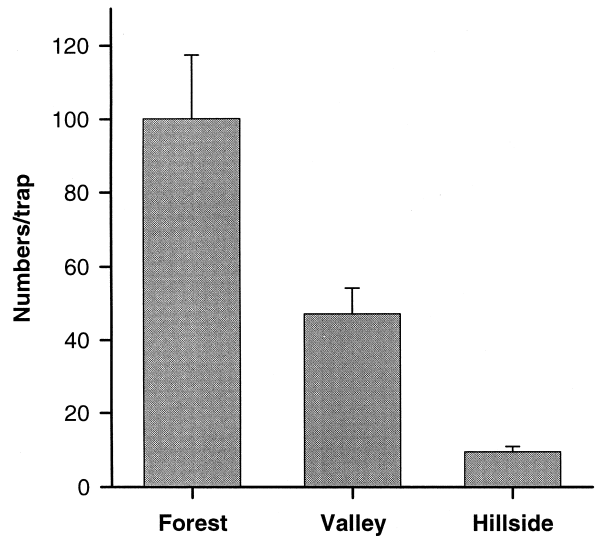
Comparisons of insect density among habitat types (forest, valley and hillside) were made with one-way ANOVA on natural log (n+1)-transformed data using traps as replicates. Subsequent pair-wise comparisons were made with the LSD test. Because caddisfly data could not be transformed successfully to homogenize variances among habitats, comparisons were made with the non-parametric Kruskal-Wallis test followed by U-tests.

Significant differences in sex ratios and the numbers of selected taxa taken in the upstream and downstream sides of Malaise traps were evaluated with Chi-square goodness of fit tests. Where multiple comparisons were made P values were adjusted by the sequential Bonferroni method to reduce the likelihood of making Type 1 errors.

Results

Continuous Malaise trapping for 9 weeks in late summer resulted in the capture of 1293 Ephemeroptera, Plecoptera and Trichoptera adults. All 51 mayflies were *Deleatidium* species (Leptophlebiidae) but the 211 stoneflies included representatives of three families and six species. Most abundant were the notonemourids *Cristaperla fimbria* and *Spaniocerca zelandica*. Caddisflies made up 79 % of the EPT catch and included 38 species in 10 families. The most strongly represented families were Hydrobiosidae (33 % of Trichoptera), Conoesucidae (27 %) and Hydroptilidae (20 %).

Ordination of the catch data (all dates combined) showed that the EPT assemblages were grouped broadly according to location within the trapping area (Fig. 2). Thus, the five traps over the stream in Reservoir Bush forest clustered together and two further groupings (upper and lower Middle Bush Stream valleys) comprised traps in grassland above and below the confluence of Reservoir Bush and Middle Bush streams, respectively. The two traps over the stream below the forest (lower Reservoir Bush Stream, Fig. 2) had assemblages intermediate in composition between those in the forest and grassland, and in particular the dominant species in the forest were proportionately much less abundant. Finally, the three traps in the riparian zone of the forest grouped together near the top of the ordination diagram.

Dominant species in the five ordination groups differed considerably with a caddisfly *Olinga jeanae* (Conoesucidae) and the stonefly *C. fimbria* most abundant in forest stream traps and other caddis species predominating in the grassland valleys (Table 1). The forest traps away from the stream collected large numbers of two Hydroptilidae species that were rarely found in other traps. The larvae of Hydroptilidae are not known to inhabit either Reservoir Bush or Middle Bush streams but do occur in Grasmere Stream and it is possible they inhabit seepages close to the forest edge.

When the results are considered in relation to the three landscape units (habitats) in which traps were set (forest, grassland valley, grassland hillside) large differences in numbers of insects trapped and proportions of the three aquatic insect orders were seen

Table 1. The three most abundant species in the five ordination groups identified in Fig. 2.

Forest stream (Reservoir Bush)	Riparian forest	Grasslnd stream (Lower Reservoir Bush)
Olinga jeanae	*Oxyethira albiceps*	*Oeconesus maori*
Cristaperla fimbria	*Paroxyethira hendersoni*	*Hydrochorema crassicaudatum*
Spaniocerca zelandica	*Hydrobiosis parumbripennis*	*Edpercivalia maxima*
Middle Bush Stream (Upper valley)	**Middle Bush Stream (Lower valley)**	
H. parumbripennis	*H. parumbripennis*	
O. maori	*Pycnocentria evecta*	
Polyplectropus aurifusca	Aoteapsyche colonica	

Table 2. Relative abundances (%) of Ephemeroptera, Plecoptera and Trichoptera trapped in forest, stream valley and hillside habitats, calculated on a per trap basis.

|	Forest	Valley	Hillside
Ephemeroptera	90.2	2.0	7.8
Plecoptera	91.9	6.2	1.9
Trichoptera	56.7	36.3	7.0

Table 3. Sex ratios (% females) of common aquatic insect taxa taken in Malaise traps including three caddisfly species without larvae in the Cass Hill streams. Significant differences ($P < 0.05$, sequential Bonferroni-adjusted) in proportions of males and females are indicated by asterisks.

	n	% female
All Ephemeroptera	51	69*
Deleatidium fumosum	45	72*
All Plecoptera	211	86*
Cristaperla fimbria	115	92*
Spaniocerca zelandica	68	84*
All Trichoptera	1031	53
Hydrobiosidae	342	49
Conoesucidae	277	63*
Hydroptilidae	206	40*
Oeconesidae	66	45
Taxa without larvae in Reservoir and Middle Bush streams		
Aoteapsyche colonica	27	96*
Pycnocentria evecta	52	85*
Olinga feredayi	27	85*

(Fig. 3, Table 2). Almost all mayflies and stoneflies were taken in forest (90.2 and 91.9 % per trap, respectively), but because of considerable between-trap variation in catch sizes the mean number of caddis taken in forest traps (70.6) did not differ significantly from that in valley traps (45.25) (Kruskal-Wallis test, followed by pair-wise U-tests; $P > 0.05$). Hillside traps, however, captured significantly fewer caddisflies (mean 8.7/trap, $P < 0.05$) than either of the other groups of traps. Despite large differences in abundance and dominance of insects among the three habitats, many species were collected in all of them. Thus, of the 38 caddisfly taxa found, 30 were taken in forest, 33 in grassland valleys and 31 in hillside traps. However, although all six stonefly species were taken in forest, only three were found in each of the other habitats. All three mayfly species were collected in forest and valleys, and two of them on hillsides.

Sex ratios

Six times more female than male stoneflies were taken in Malaise traps and for the two most common species, *C. fimbria* and *S. zelandica* the difference was highly significant (Table 3). Female mayflies were also more abundant than males, the difference being significant for the most abundant species *D. fumosum*. Similar numbers of subimaginal and adult females of this species were collected, but all males were adults.

In contrast to mayflies and stoneflies only 53 % of all caddisflies were female; however, sex ratios varied considerably among families and species (Table 3). Of the four most abundant families the proportion of trapped females ranged from 40 to 63 %, with only the Hydroptilidae having a significantly greater abundance of males.

Because we were interested in the sex of individuals dispersing away from streams, sex ratios of caddisflies caught in 18 traps on the hillside and along the dry stream beds were determined as well. Too few mayflies (4) and stoneflies (19) were found in these groups of traps for analysis to be worthwhile. However, of 393 caddisflies taken in them, 56 % were female, including 64 % of those on the hillside. Three
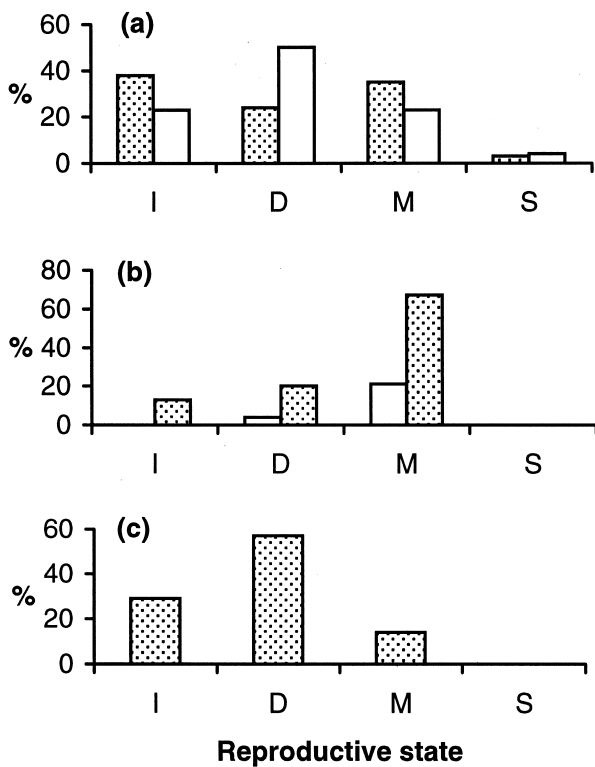
Fig. 4. Reproductive stage of female caddisflies captured in selected Malaise traps (see text for details). Stages are I, immature; D, developing (no mature eggs); M, mature (eggs fully developed); S, spent (eggs laid). **(a)** *Pycnocentria evecta* (stippled bars, n = 37), *Aoteapsyche colonica* (open bars, n = 22); **(b)** *Hydrobiosis parumbripennis* (Stippled bars, n = 25), *Edpercivalia fusca* (open bars, n = 15); **(c)** *Olinga jeanae* (n = 28).

Table 4. Percentages of 8 common species (and their females, separately) entering the upstream sides of Malaise traps set over the stream. Results of Chi-square tests comparing numbers of insects entering the two sides of traps are also shown. Significant probabilities (P < 0.05, sequential Bonferroni-corrected) are indicated by asterisks.

Taxon	All adults		Females	
	%	χ^2	%	χ^2
Forest stream				
Deleatidium fumosum	67.5	4.9	67.9	3.57
Cristaperla fimbria	52.8	0.34	53.0	0.36
Spaniocerca zelandica	68.3	8.40*	76.5	14.3*
Olinga jeanae	62.6	9.81*	72.0	15.8*
Edpercivalia fusca	66.7	4.0	66.7	3.33
Hydrochorema crassicaudatum	61.3	1.58	66.7	2.33
Dry lower valley				
Hydrobiosis parumbripennis	74.3	8.26*	80.0	3.6
Pycnocentria evecta	70.6	5.76*	71.4	5.14

were all taken in traps over the stream and were in various stages of development (Fig. 4 c). Few were fully mature and about one third had very limited ovariole development so had probably just emerged.

Flight direction

Numbers of adults of the six most abundant species entering Malaise traps set over the stream channel where flowing surface water was present are shown in Table 4. All six species were taken principally in the forested section of the stream where their larvae mainly occur. Data for two further species (*H. parumbripennis* and *P. evecta*) whose larvae are abundant in Grasmere Stream but not in the Cass Hill streams (Death 1991; authors' observations) are also shown. All eight species had a tendency to enter traps from upstream (52.8–74.3 % of individuals), although the difference in direction of entry was significant for only four species (Table 4). When females were considered, separately, they were also found to enter traps predominantly from upstream (Table 4).

Discussion

Although the direction and magnitude of dispersal varies greatly among aquatic insect species, local landscape features and environmental gradients are believed to play a central role in dispersal behaviour (Bohonak & Jenkins 2003). The distribution of adult mayflies, stoneflies and caddis in our study area was influenced by vegetation and valley morphology, most obviously grassland-scrub v forest, but also valley v exposed hillside. To an extent the distribution of

species whose larvae did not inhabit Reservoir and Middle Bush streams (*Aoteapsyche colonica*, *Pycnocentria evecta* and *Olinga feredayi*) were taken in the two traps (L2, L3) closest to Grasmere Stream where their larvae are common. In all three species females were significantly more abundant than males (Table 3).

Reproductive state of females

Females of the five species examined showed contrasting states of reproductive development. Many *Pycnocentria evecta* and *Aoteapsyche colonica*, were not fully developed (62 % and 73 %, respectively; Fig. 4 a) and were likely flying inland from Grasmere Stream to mature. In contrast, most females of the hydrobiosids *Hydrobiosis parumbripennis* and *Edpercivalia fusca*, who natal streams were uncertain, were packed with fully developed eggs (Fig. 4 b) and were more likely to have been searching for oviposition sites. Females of the forest-dwelling *Olinga jeanae*

individual species reflected the distributions of their larvae, but many adults were found tens or hundreds of metres from the nearest known larval habitat.

Plecoptera

Most stoneflies were captured in traps set over the stream within Reservoir Bush, and the two abundant species *Spaniocerca zelandica* and *Cristaperla fimbria*, which have predominantly forest-stream-dwelling nymphs, were taken rarely outside the forest. Furthermore, none were collected on the hillside away from the stream channels. These findings are consistent with those of Winterbourn (2005) who found that these two stoneflies rarely dispersed beyond the riparian zone of a nearby forest stream. The strongly female-biased sex ratios of the stoneflies are unlikely to reflect the true proportions of males and females in the population. Rather, they probably reflect the timing of our study in the second half of the main emergence period when more females may be emerging from the stream and earlier-emerging females are returning to it to oviposit (Winterbourn 2005). Although significantly more adults of *S. zelandica* had entered traps on the upstream side, no downstream trend in numbers of adults trapped was found and only a single adult was taken in the lower valley section of the stream. Winterbourn & Crowe (1999) suggested that many of the *S. zelandica* adults found on the upstream sides of sticky traps that were touching the water may have been floating downstream following emergence, but because our Malaise traps were not in contact with the water it is likely that local flights of adults were more frequently in a downstream direction.

Ephemeroptera

The leptophlebiid *Deleatidium fumosum* was the only moderately abundant mayfly taken by Malaise trapping and like the stoneflies most winged individuals were found in the forest despite nymphs being abundant in the grassland reaches. Adults and subimagos were both susceptible to capture although an absence of subimaginal males suggests they may not fly or move far from their emergence sites. Little is known about the behaviour of adult (and subimaginal) mayflies, including *Deleatidium* species, at small forest streams in New Zealand, but our general observations over many years suggest an absence of mass emergence and swarming where a forest canopy occurs. As mayflies were not captured in the dry stream reaches, we obtained no evidence of low-flying dis-

persal in any direction along these "natural corridors". Lynch et al. (2002) rarely captured mayflies in Malaise traps set alongside streams in northern Australia, despite good captures on sticky traps 2 m above the stream channels. Their findings and ours suggest that Malaise traps may be a poor choice for studies of dispersal of some species of mayfly.

Trichoptera

Although caddisflies were most abundant in forest traps, large numbers were also taken in the grassland valleys, although not on the higher hillside. The species taken in most traps (*Oeconesus maori* and *Hydrobiosis parumbripennis*) have larvae that are widely distributed in forest and grassland streams in the study area, but *Olinga jeanae*, the most abundant forest-dwelling species, was rarely taken outside the forest. At Cass its larvae appear to be restricted to forest streams, whereas those of *O. feredayi*, whose adults were almost all taken in grassland, inhabit nearby Grasmere Stream. The two congeneric species therefore appear to partition the local environment in both larval and adult stages. Similarly, the nymphs of two mayflies *Nesameletus ornatus* and *N. austrinus* have non-overlapping distributions in this same set of streams with the latter restricted to the forest and the former in the more open grassland-scrub (Winterbourn 2003).

Our results suggest that valleys, including those containing dry stream channels, are important corridors for dispersal of caddisflies. Fortuitously, most of Middle Bush Stream within the study area was dry throughout the duration of our study, except for a very short (< 50 m) section of surface flow below the entry of Reservoir Bush Stream. Furthermore, it had been dry for most of the previous seven years so that larval populations were absent and this section of stream could not have been a source of adult insects taken in our traps, six of which were sited over the dry channel and two others beside it. Caddisflies taken in the dry valley of Middle Bush Stream are likely to have come from further upstream where flow is permanent and where their larvae are known to live, and also from Grasmere Stream further down the valley. Thus, the larvae of some species taken in the lowermost dry valley traps, notably *Aoteapsyche colonica*, *Pycnocentria evecta* and *Olinga feredayi* are common in Grasmere Stream but normally absent from Middle and Reservoir Bush streams (Death 1991; authors' observations). These three species, which were taken up to 300 m from their larval habi-

tat were also found to be strong dispersers by Collier & Smith (1998).

We also found that the dispersing adults of all three species were predominantly females (84–97%), which may have been in search of oviposition sites, or flying inland to mature following emergence (Svennson 1974). Our dissections of *P. evecta* and *A. colonica* taken in the lower dry valley indicated that a majority did not have fully mature eggs and therefore would not have been flying to streams to lay eggs. In contrast, almost all hydrobiosids, whether taken close to or far from streams had their abdomens packed with mature eggs and therefore, were more likely to be searching for oviposition sites.

Over 50 years ago Muller (1954) proposed that the adults of stream insects should fly upstream to oviposit and thereby compensate for the downstream displacement of larval populations by drift; recently, there has been considerable interest in testing this hypothesis. Several studies of stable isotope-labeled insects have demonstrated a preponderance of upstream flight in mayfly and stonefly species (Hershey et al. 1993, MacNeale et al. 2005) and several forest-dwelling caddisflies were more abundant on the downstream sides of sticky traps set across a New Zealand stream, suggesting net upstream movement of adults (Winterbourn & Crowe 1999). The findings of our present study using Malaise traps are of interest because none of the species considered entered the traps in greater numbers from the downstream side and four were significantly more abundant on the upstream side. These data suggest that either pronounced upstream flight is not a characteristic of these species, or that Malaise trap catches are simply consequences of small-scale local movements and do not provide a useful indication of directional dispersal. We agree with MacNeale et al. (2005) that instantaneous catches on particular sides of directional traps are not necessarily good indicators of directional flight, or net indicators of population movement, and conclude that reliable estimates of dispersal direction and distance requires direct marking of individuals. Knowledge of the behavioural responses of adult insects to environmental factors including air temperature, wind speed and direction (factors that were not examined in our study) can also be expected to improve understanding of individual and population movements of adult stream insects at multiple scales.

Conclusions

Our results showed that the distributions of some mayflies, stoneflies and caddisflies were restricted to forest or grassland-scrub, whereas others occurred within both kinds of vegetation. Most low-flying caddis in particular, appeared to disperse primarily along stream channels and valleys, even where surface water was absent, although it is possible that higher flying individuals and species may disperse more widely. Some species, particularly stoneflies, did not disperse far from their natal streams, but some caddis were trapped hundreds of metres from their most probable sources. The reproductive status of dispersing females suggested that some may fly away from their natal streams to mature, whereas others may disperse widely in search of oviposition sites. When long-distance dispersers (both males and females) colonize new habitats they could have a significant role in exchanging genetic material among populations, especially if very few egg-laying females are needed to establish a local larval population (Schmidt et al. 1995).

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