

1 **Dispersal traits may reflect dispersal distances, but dispersers may not connect populations**  
2 **demographically**

3

4

5 Jill Lancaster and Barbara J. Downes

6 School of Geography, University of Melbourne, 221 Bouverie Street, Parkville, VIC, Australia

7

8

9

10 **Author for correspondence:**

11 Jill Lancaster, School of Geography, University of Melbourne, 221 Bouverie Street, Parkville, VIC

12 3010, Australia

13 email: JillL@unimelb.edu.au

14

15

16 **Running head:** Dispersal traits and effective dispersal

17

18 **Author Contributions:** JL and BJD collected samples; JL measured wings; JL and BJD analyzed the  
19 data and wrote the manuscript.

20

21 **Abstract**

22 Ecological traits that reflect movement potential are often used as proxies for measured dispersal  
23 distances. Whether such traits reflect actual dispersal is often untested. Such tests are important  
24 because maximum dispersal distances may not be achieved and many dispersal events may be  
25 unsuccessful (without reproduction). For insects, many habitat patches harbour ‘resident’ species that  
26 are present as larvae (sedentary) and adults (winged and dispersing), and ‘itinerant’ species present  
27 only as adults that have dispersed from elsewhere and fail to reproduce. We tested whether itinerancy  
28 patterns were temporally consistent, and whether itinerant and resident species differed in wing  
29 morphology, a strong correlate of flight capability. Over 3 years and at multiple locations in a 22 km  
30 stream length, we sampled larvae and adults of caddisflies in the genus *Ecnomus* to categorize species  
31 as residents or itinerants. Flight capacity was measured using wing size (length and area) and shape  
32 parameters (aspect ratio and the second moment of wing area). Three species of *Ecnomus* were  
33 residents and three species were itinerants, and patterns were consistent over 3 years. On average,  
34 itinerant species had larger wings, suggesting a greater capacity to fly long distances. Wing shape  
35 differed between species, but did not differ systematically between residents and itinerants. Wing  
36 morphology was associated with actual but not effective dispersal of some species of *Ecnomus*.  
37 Morphological traits may have weak explanatory power for hypotheses regarding the demographic  
38 connectedness of populations, unless accompanied by data demonstrating which dispersers contribute  
39 new individuals to populations.

40

41 **Key-words:** aspect ratio, Ecnomidae, insect flight, moment of area, Trichoptera, wing morphology

42

43 **Introduction**

44

45 The spatial distribution of organisms across the landscape is a function of the distribution, size and  
46 relative abundance of suitable habitat patches, coupled with the capability of organisms to disperse  
47 and colonize patches. Knowing how far and how often organisms disperse is necessary to answer  
48 many ecological questions, for example in the contexts of metapopulations, metacommunities,

49 invasion ecology and biogeography. It is equally important, for many questions, to know whether and  
50 when dispersal results in populations that are connected demographically, i.e. when dispersal is  
51 accompanied by successful reproduction. Despite the obvious importance of dispersal, there is a  
52 paucity of information on dispersal rates, distances and the demographic outcomes of dispersal for  
53 most species. This constrains our ability to test many hypotheses directly. In the context of  
54 demography, dispersal can be defined broadly as the tendency of an organism to reproduce away from  
55 its birth place (Levin et al. 2003), or the movement of an organism from its place of origin to a place  
56 where it reproduces or would reproduce if it survived and conditions were suitable for reproduction  
57 (e.g. presence of mates, nesting or egg-laying sites). ‘Actual dispersal’ describes movement of  
58 individuals irrespective of whether reproduction occurs (e.g. inter-patch movement) whereas ‘effective  
59 dispersal’, a subset of actual dispersal, describes successful reproduction of an individual that has  
60 dispersed (i.e. recruitment). Distinguishing between the two is important ecologically. In the context  
61 of community assembly, for example, the set of actual dispersers defines a regional or geographical  
62 species pool whereas effective dispersers define the local species pool, i.e. the observable community  
63 (Zobel 1992; Belyea and Lancaster 1999). The difference between the two defines the set of potential  
64 colonists that have been excluded from the local species pool by environmental or biotic constraints.  
65  
66 Species with individuals that disperse to some locations without reproducing we call ‘itinerants’. In  
67 contrast, ‘residents’ are species that occur at the same locations, that reproduce successfully, and that  
68 may comprise both dispersing and non-dispersing individuals. Note that our focus is on the occurrence  
69 of dispersers at times and habitat patches where reproduction or recruitment could occur; we omit  
70 species, often referred to as itinerants, occurring at non-breeding times or locations for other activities,  
71 such as migratory birds foraging at over-wintering grounds (e.g. Morrison et al. 2013). Additionally,  
72 we distinguish between itinerant and vagrant species in this study: vagrant individuals are typically  
73 outside their normal range and occur only rarely and in very low numbers, whereas itinerants are often  
74 numerous and occur frequently or regularly at potential breeding sites, but where they do not  
75 reproduce. Following these definitions, itinerants are species where some individuals routinely move  
76 between habitat patches, but fail to colonize some locations. Thus, in any habitat patch there may be

77 some dispersing individuals that originate from local breeding populations (residents) and some from  
78 distant populations (itinerants). Numerous studies have documented species belonging to these  
79 categories across a range of organisms and ecosystems, including insects (McCauley 2006), birds  
80 (Schoener et al. 2005) and freshwater fish (Humphries et al. 2008).

81

82 When considering the potential role of dispersal in population and community dynamics, one  
83 approach is to explore the differences between species that make some more likely to colonize new  
84 habitat patches than others (e.g. Sakai et al. 2001). For example, an association between the  
85 morphology and dispersal potential of wind-dispersed plant seeds is well documented (Vittoz and  
86 Engler 2007). In this study, we tested whether dispersing individuals of resident and itinerant species  
87 have different morphological traits related to dispersal potential, which we define as the capacity to  
88 travel long distances. At any particular location, determining dispersal distances of resident species is  
89 difficult because dispersing individuals could arise locally (i.e. very short travel distances) or from  
90 distant populations. Itinerants, however, must have travelled from elsewhere and thus are likely, on  
91 average, to have travelled longer distances than most residents; it follows that itinerant individuals  
92 should, on average, have greater dispersal capabilities than residents, which should be reflected in  
93 differences in dispersal-related morphology. However, this finding would also show that traits  
94 associated with strong dispersal potential may not be associated with demographic outcomes. If  
95 correct, this suggests that between-patch dispersal is not necessarily evidence of demographic  
96 connectedness. Such an outcome is ecologically important because many studies that compare species  
97 based on their dispersal traits assume implicitly that dispersal capability can be used to infer connected  
98 populations (review: Lowe and McPeck 2014).

99

100 Many insects have larvae that are relatively sedentary and restricted to patches of suitable habitat, and  
101 dispersal occurs in the adult stage and involves flight between habitat patches. Thus, itinerant insects  
102 can be defined as species that are present as adults but not as larvae (i.e. no evidence of successful  
103 reproduction), whereas residents are present as both larvae and adults. Aquatic insects are model study  
104 organisms in this context because, typically, larvae are long-lived and restricted to the aquatic

105 environment whereas adults are short-lived, terrestrial, winged and the major dispersal stage. Larvae  
106 of lentic species (inhabiting standing waters such as ponds and lakes) have little potential to colonize  
107 different water bodies (except via zoochory (Bilton et al. 2001)), whereas larvae of lotic species  
108 (inhabiting running waters of streams and rivers) could – theoretically – disperse downstream by  
109 drifting with the current. Most genetic studies of dispersal in aquatic insect populations have shown,  
110 however, that flight is the major dispersal mechanism (e.g. Hughes 2007) and the aquatic stages of  
111 many taxa may drift only rarely or travel short distances (e.g. Schreiber 1995; Downes and Lancaster  
112 2010; Lancaster et al. 2011).

113

114 Flight distances are difficult to quantify directly in natural environments, especially for insect taxa  
115 with small-bodied adults that are largely nocturnal or inhabit dense vegetation. Alternatively,  
116 morphologic characters of wings can provide proxy measures of flight capability, because wings are  
117 high-lift structures and the magnitude of lift varies with wing morphology. The diversity of wing  
118 morphology among insect taxa is matched by functional divergence in wing kinematics (wingbeat  
119 motions) and in the underlying aerodynamics of flight (Dudley 2000). The importance and suitability  
120 of wing size and shape for comparing flight capability among species has been recognized for decades  
121 (e.g. Weis-Fogh 1973; Ellington 1984a) even though many aspects of the aerodynamics of insect  
122 flight remain unresolved (Dudley 2000; Floreano et al. 2010; Hedrick et al. 2015). Wing morphology  
123 cannot capture all aspects of flight capability and species may differ in other traits (e.g. kinematics,  
124 physiology, behaviour) that can influence flight, especially if species are distantly related. Thus, it is  
125 prudent to focus on species within a narrow phylogenetic range and thereby minimize the possibility  
126 that unmeasured traits might confound interpretations based on wing morphology. Quantifying  
127 morphological parameters is more practicable than many other aspects of flight, and wing morphology  
128 has been used to test various ecological and evolutionary hypotheses regarding flight capability of  
129 diverse insects, including Lepidoptera (Betts and Wootton 1988), Odonata (Serrano-Meneses et al.  
130 2008; Outomuro et al. 2013) and Diptera (Ribak et al. 2009). However, there are few empirical tests  
131 using field data that demonstrate an association between wing morphology and actual dispersal  
132 distances (but see Sakar 2012). Such field tests are difficult to devise, but essential to determine the

133 veracity of assumptions underpinning tests that use putative dispersal traits to test ecological  
134 hypotheses. For example, when considering the flight or dispersal capabilities of any organism, it is  
135 important to distinguish between the ‘dispersal distance’ and the ‘travel distance’. We define dispersal  
136 distance as the straight line or vector distance between a dispersing individual’s place of origin to a  
137 place where it reproduces or would reproduce if it survived and conditions were suitable for  
138 reproduction; travel distance is the total path length an individual travelled during a dispersal event,  
139 i.e. including all the twists and turns. These definitions make clear that an organism’s capability to  
140 travel long distances may not necessarily be associated with a tendency to disperse long distances.

141

142 The aims of this field study were to test whether morphological traits of some aquatic insects that are  
143 currently used to infer a capacity to fly long distances, differ between itinerant and resident species,  
144 i.e. between species known to have dispersed different average distances. If our results support this  
145 hypothesis, then we will have provided a field test confirming the oft-used assumption that dispersal  
146 traits (e.g. wing morphology) can be a proxy for travel and dispersal distances. Simultaneously,  
147 however, the same outcome would suggest that dispersal traits do not necessarily indicate whether  
148 populations are connected demographically, and this raises important questions about whether  
149 dispersal traits are suitable to address many ecological questions. In this study, measures of wing  
150 morphology comprised two gross parameters, wing area and length, and two shape parameters, wing  
151 aspect ratio and the second moment of wing area. These metrics reflect aspects of aerodynamic  
152 performance according to well-established models of insect flapping flight (Weis-Fogh 1973;  
153 Ellington 1984a, 1984b). If itinerants are better dispersers than resident species (i.e. have the  
154 capability to fly longer distances) then, on average, itinerants were expected to have larger wings  
155 and/or wing shapes better suited for long-distance flight. Before comparing wing morphologies,  
156 however, we must first identify species that classify as residents and itinerants, and evidence from  
157 multiple sites and times is required to demonstrate that itinerancy patterns are persistent (absence of  
158 such evidence would suggest that itinerancy is rare or unimportant). Tests of our hypothesis do not  
159 require us to sample itinerants at locations where they are residents because we do not pose questions  
160 about the causes or evolutionary origin of any potential differences between species. In the text to

161 follow, it is implicit that ‘resident species’ refers to adults collected at sites where larvae are present,  
162 ‘itinerant species’ refers to dispersing individuals found at sites where there is no recruitment.

163

164

## 165 **Methods**

### 166 *Study species, site and sampling protocols*

167 Our study focused on species within a single genus of Trichoptera, *Ecnomus* McLachlan  
168 (Ecnomidae). This genus is diverse and widespread throughout Australia and multiple species often  
169 co-occur (Cartwright 1990), thus maximizing the possibility that several closely-related species would  
170 fit in each category, as required for hypothesis tests. Our preliminary observations suggested that both  
171 resident and itinerant species occurred in some locations, as observed for Trichoptera in other systems  
172 (e.g. Svensson 1974; Sode and Wiberg-Larsen 1993). Several species of *Ecnomus* co-occurred in the  
173 study stream, suggesting some similarities in habitat and resource requirements. All reliable records of  
174 larvae of these species are from running waters, suggesting that these species inhabit only lotic  
175 environments (Atlas of Living Australia <http://www.ala.org.au/>). The adults are small bodied ( $\approx 1$  cm  
176 length), but large enough that flight occurs at high Reynolds numbers,  $Re \gg 10^2$  (flight is  
177 aerodynamically different at low  $Re$ ). Ecnomid adults generally fly at night, but not during cold or  
178 windy conditions. Wing venation and articulation is almost identical for these species so there are  
179 unlikely to be differences in wing movement, deformation and bending. The net-spinning larvae of  
180 *Ecnomus* are omnivorous but prey primarily upon invertebrates that become entangled in the silken  
181 threads of the net (Chessman 1986; Lancaster et al. 2009). In the study stream, larvae occur  
182 throughout the year, the adult flight period is approximately 6 months (Nov-April) and oviposition  
183 occurs throughout (see also Macqueen and Downes 2015). These observations suggest that these  
184 species may be bi- or multivoltine, have weakly synchronized cohorts with long emergence periods,  
185 overlapping generations, and perhaps relatively long-lived adults (e.g. up to two weeks).

186

187 The study was carried out in a 22 km length in the headwaters of Hughes Creek, a sandy-bed stream in  
188 central Victoria, south-eastern Australia. There were no major tributaries along this length. Sample

189 sites were in the upper reaches (36° 59' S; 145° 21' E) where the stream runs off the granite batholith  
190 of the Strathbogie Ranges and before reaching the floodplain of the Goulburn River. There were 12  
191 sample sites (each site a 40 m channel length), at altitudes ranging from 355 to 242 m ASL, and  
192 spaced on average 1.6 km apart (range 0.6 to 3.7 km) along the study length. Sampling multiple  
193 locations minimizes the risk that results are unduly influenced by locations that are suitable for adults  
194 but not larvae, and *vice versa*. Above our study length, Hughes Creek becomes narrow and swampy  
195 and at its most upstream area becomes a series of spring-fed pools (>6 km from our most upstream  
196 sample site). The distance between our most upstream site and the headwaters of the nearest creek  
197 (Seven Creeks) is ≈18 km in a straight line and >60 km if dispersing individuals follow stream  
198 corridors. The nearest at least semi-permanent creek to our most downstream site on Hughes Creek is  
199 ≈16 km away in a direct line (Creightons Creek). Detailed information on channel morphology,  
200 physicochemistry, vegetation cover, etc is available elsewhere (e.g. Lancaster et al. 2009; Downes et  
201 al. 2011; Lancaster and Downes 2015; Downes et al. in press). Longitudinal environmental gradients  
202 along the study length included an increase in water temperature accompanying increasing channel  
203 width, decreasing water depth and reduced shade from a dwindling riparian zone. The most upstream  
204 sites were located in areas with relatively intact riparian vegetation and in a moderately well-treed  
205 landscape, and within a few km of other creek headwaters and freshwater springs. With distance  
206 downstream, stream populations become increasingly isolated as the valley in which the stream lies  
207 becomes incised and the land is increasingly altered for grazing (e.g. loss of tree cover, decreased  
208 riparian zone). Nevertheless, these environmental gradients limit the distribution of only a few species  
209 in Hughes Creek (Lancaster and Downes 2017; Downes et al. in press).

210

211 All sites were sampled in summer (January or February) and during the breeding season in three  
212 consecutive years (2013, 2014, 2015) to determine the relative abundance of larval and adult  
213 *Ecnomus*, and to categorize species as residents or itinerants. We have sampled benthic and adult  
214 insects from this stream over multiple years and in multiple seasons (references above and  
215 unpublished data), and have observed no seasonal turnover in the presence/absence of species as



216 larvae and no species-specific variations in flight period. Thus, we are confident that sampling larvae  
217 and adults only in summer (middle of the flight period) is adequate to describe the assemblage of  
218 *Ecnomus* spp. in this stream. In this study, larvae and adults were collected contemporaneously and  
219 within one week in the first two years; in 2015 larvae were sampled 3 weeks later than adults, but this  
220 time lag is unlikely to influence hypothesis tests. On each occasion, larvae were collected with a  
221 Surber sampler (0.09 m<sup>2</sup>, 250 µm mesh): 10 samples per site in 2013, 15 samples per site in 2014 and  
222 2015. Samples were located within each of the 12 sites according to a random stratified design, with  
223 roughly one quarter of the samples located within each 10 m segment of the 40 m site. Samples were  
224 composited and then subsampled to provide a single estimate of larval densities per site. Composited  
225 samples of invertebrates were split into 100 aliquots using a sample splitter (Marchant 1988), and 20  
226 aliquots were selected at random for enumeration. Invertebrates were sorted under a stereomicroscope  
227 and all 3rd to 5th instar larval *Ecnomus* were identified to species (early instars cannot be identified to  
228 species with confidence) (Cartwright 1997). Adult caddisflies active locally at each site were sampled  
229 using light traps placed at the water's edge and within the flight boundary layer, where flight is  
230 intentionally directed and wind-assisted dispersal is rare (Dudley 2000). All individuals were sexed  
231 and identified to species (Neboiss 1986; Cartwright 1990). All 12 sites were sampled in 2013 and  
232 2014; only 8 sites were sampled in 2015 (see Results). Light traps comprised a white, plastic tray (28  
233 x 22 x 5 cm) with 70% ethanol to a depth of approx. 1.5 cm. A fluorescent, ultraviolet blacklight (6  
234 Watt, 12 volt, 225 mm long tube) was laid across the top of the tray, which was placed inside a black  
235 plastic tub (diameter = 39 cm; height = 32 cm). This ensured that light did not spill sideways but was  
236 directed upwards in order to attract only insects flying nearby (Collier and Smith 1998). Because the  
237 efficacy of light traps is sensitive to insect responses to daily weather variations, the number of traps  
238 deployed and number of trapping nights required to collect adequate numbers of insects varied  
239 between sites. In 2013, three traps were deployed at each site for 2 hours, beginning 30 minutes before  
240 sunset. In 2014 and 2015, trapping intensity was increased as required by the weather (more traps or  
241 more nights per site) to ensure large sample sizes. Because comparisons of abundance data across  
242 years and sample sites focused on species relative abundances, differences in the number of specimens  
243 collected are unimportant.

244

245 *Morphological measurements*

246 Analysis of comparative wing morphology focused on two gross parameters or first-order descriptions  
247 of morphology, wing area and wing length (or wing span), and on two shape parameters or second  
248 order descriptions, wing aspect ratio (AR) and the non-dimensional radius of the second moment of  
249 wing area,  $\hat{r}_2(S)$ . In general, lift forces (and hence flight capability) increase with wing size (span;  
250 area). In terms of wing shape, high AR reflects slender wing shapes, which are associated with power  
251 economy and extended flight, whereas broad wings have a low AR, which favours slow, agile flight  
252 (Betts and Wootton 1988; Dudley 2000). Values of  $\hat{r}_2(S)$  are low for wings that have broad bases and  
253 narrow tips and values increase as the broadest part of the wing shifts towards the tip. Wings with very  
254 broad tips and high  $\hat{r}_2(S)$  may confer agility and maneuverability, but also increase the energetic  
255 power required for flight (Ellington 1984b). Conversely, wings with lower values of  $\hat{r}_2(S)$  (broad  
256 bases, or leading and trailing edges that are approximately parallel) may be better suited for extended  
257 or long-distance flight. These parameters have all been used successfully to compare flight capability  
258 among various insect species (references above). We did not measure wing loading because this  
259 parameter is more closely related to flight *speed* not flight distance (Dudley 2000). Furthermore,  
260 interpreting wing loading in terms of species' relative flight capacity can be difficult without  
261 information on the relative contribution of different tissues to total body mass (e.g. flight muscle, fat  
262 body, cuticle).

263

264 One pair of fore and hind wings were removed from each insect, mounted on a microscope slide and a  
265 digital image produced. Wings were oriented so that wing span or maximum wing length was  
266 horizontal and perpendicular to the longitudinal axis of the insect body (Fig. 1) and the hind wing was  
267 oriented in the coupled position (Stocks 2010). Wing measurements were carried out on digital images  
268 of coupled wing pairs in planform (the orientation of wings during the down stroke and the generation  
269 of lift forces) and using the software ImageJ 1.49s (Rasband 1997–2012). There were five replicates  
270 for each species/sex combination, except measurements of wing length where N = 12. Replicate  
271 specimens were selected from a wide range of year/site combinations to avoid inadvertently selecting

272 closely related individuals. Wing length,  $R$ , is the distance from the wing base to the tip of the fore  
273 wing. Wing area,  $S$ , was measured directly in ImageJ and multiplied by 2 to account for both pairs of  
274 wings.

275

276 Wing aspect ratio (AR) is a nondimensional representation of wing shape describing the wing length  
277 relative to its width, and is calculated as:

$$AR = \frac{4R^2}{S}$$

278

279 The moments of wing area indicate how the area is distributed along the wing length, or the shape of  
280 the wing in planform. The second moment of wing area and its non-dimensional radius was calculated  
281 following Ellington (1984a). The  $k$ th moment of wing area,  $S_k$ , requires measurements of the wing  
282 chord,  $c$ , at various distances or radii,  $r$ , along the wing span,  $R$ , (Fig. 1) and is described by the  
283 equation:

$$S_k = 2 \int_0^R cr^k dr$$

284 For a given wing span and area, the moments of area depend only on the distribution of chord lengths  
285 along the wing. For each coupled wing pair, 50 measures of  $r$  and  $c$ , spaced evenly along  $R$ , were used  
286 to calculate moments of wing area, using the equation above. The nondimensional radii of the  
287 moments of wing area provide parameters of shape that can be compared between taxa and are  
288 calculated as:

$$\hat{r}_k = \sqrt[k]{\frac{S_k}{SR^k}}$$

289 According to Weis-Fogh (1973), in a quasi-steady model of flight the second moment of wing area,  
290  $\hat{r}_2(S)$ , is proportional to the mean lift force of the wings, and the third moment,  $\hat{r}_3(S)$ , is proportional  
291 to the mean profile power. Because the first three moments of wing area ( $k = 1, 2, 3$ ) are strongly  
292 correlated (Ellington 1984a), it is sufficient to focus on one moment of area for the purpose of species  
293 comparisons, and we focus on  $\hat{r}_2(S)$ .

294

295 *Statistical analyses*

296 Differences between species and sexes in wing size and shape were tested using two-way ANOVA  
297 (species and sexes as orthogonal fixed factors). These tests were followed by a priori, pair-wise  
298 comparisons (Sokal and Rohlf 1981) testing for differences between groups of species that were  
299 categorized as residents and itinerants. All species were sexually dimorphic (see Results) so pair-wise  
300 comparisons were conducted separately for each sex and within the interaction (i.e. Species x Sex)  
301 term. These comparisons thus used the mean square error to create the tests – this is appropriate  
302 because Species is a fixed (not random) factor. Although samples were collected over multiple sites  
303 and years, site and year are not factors of interest to our hypothesis tests and were not included in the  
304 analyses.

305

306 For each species and year, sex ratios were calculated using specimens pooled over all sites, and  
307 differences between species were tested using one-way ANOVA with years as replicates. This test was  
308 followed by a priori, pair-wise comparisons testing for differences between groups of species that  
309 were categorized as residents and itinerants. Data were arcsine square-root transformed before  
310 analysis, as is appropriate for data that are proportions (Sokal and Rohlf 1981).

311

312 **Results**

313 Seven species of *Ecnomus* were collected in the 22 km length of Hughes Creek; three resident, three  
314 itinerant and one vagrant species. Relative abundances varied along the longitudinal stream gradient  
315 and patterns were broadly the same in each year (Table 1). The three resident species, *E. continentalis*  
316 Ulmer, *E. pansus* Neboiss and *E. cygnitus* Neboiss, were present as both larvae and adults. *Ecnomus*  
317 *continentalis* was numerically dominant at most sites, *E. cygnitus* was more abundant at upstream sites  
318 whereas *E. pansus* was more abundant downstream. These patterns are consistent with previous  
319 research on Hughes Creek and another nearby river (Seven Creeks), which also showed an association  
320 between larval and adult abundances for *E. continentalis* and *E. pansus* (no information on *E. cygnitus*:  
321 Downes et al. in press). The three itinerants, *E. russellius* Neboiss, *E. tillyardi* Mosely and *E. turgidus*

322 Neboiss, were present as adults, but never as larvae. The only exception was *E. russellius* where one  
323 larva was found in each of 2013 and 2014, and three larvae in 2015. In contrast, adults of this species  
324 were collected every year, in multiple locations and often in large numbers. Thus, *E. russellius* may  
325 very occasionally colonize upstream sites, but recruitment appears to be exceedingly rare. Itinerants  
326 were most abundant at upstream locations where they could comprise over 50% of the adult  
327 assemblage. However, itinerants were present at all sites and occasionally were plentiful at sites that  
328 were most distant from headwaters. *Ecnomus tillyardi* was the most abundant itinerant species. Only  
329 one adult specimen of *E. myallensis* Cartwright was collected over the three years (Site 12, 2014) and  
330 it appears to be a true vagrant.

331

332 Sex ratios differed between species with either equal numbers of males and females, or more females  
333 than males caught over the three years (Fig. 2). Differences between species were statistically  
334 significant ( $F_{5,12} = 4.84$ ,  $P = 0.012$ ), but pair-wise contrasts revealed no difference in sex ratios  
335 between resident and itinerant species ( $F_{1,12} = 1.96$ ,  $P = 0.187$ ).

336

337 All species were sexually dimorphic with respect to all measures of wing size and shape (Table 2, Figs  
338 3a, 4). Relative to males, females were generally larger (longer wings and larger wing area) and had  
339 slender wings with low lift force and energy-efficient flight (high AR, low  $\hat{r}_2(S)$ ). There were  
340 significant differences between species in all measures of wing size and shape (Table 2, Figs 3a, 4),  
341 but wing shapes of species within the genus *Ecnomus* were very similar to one another compared with  
342 caddisflies from other families (Fig. 3). Within each species/sex combination, coefficients of variation  
343 in shape,  $\hat{r}_2(S)$ , were very low and typically  $< 1\%$ . Shape and size parameters were correlated across  
344 species/sex combinations suggesting that shape did not change independently of size (Table 3). The  
345 directions of these correlations indicate that changes in shape that facilitate long-distance flight were  
346 accompanied by an increase in wing size, which also increases flight capability. Comparing species  
347 groups, resident and itinerant species did not differ in wing shape (no difference in AR or  $\hat{r}_2(S)$   
348 between groups), but did differ significantly in wing size (Table 2): itinerants had longer wings and  
349 larger wing areas, suggesting a capacity to fly longer distances than residents.

350

351 **Discussion**

352 Itinerant species were more likely than residents to have morphological traits associated with a  
353 capacity for long-distance flight in congeneric species of caddisfly (genus *Ecnomus*). This is  
354 consistent with the notion that inter-patch movement may be common for itinerants, even though they  
355 fail to colonize some locations. Dispersal traits that describe flight capability appeared to be associated  
356 with actual dispersal distances for these species because itinerants would have had to travel and to  
357 disperse longer distances – on average – than residents. Many itinerants were found at our upstream  
358 sites even though the closest stream across the catchment boundary was 18 km away in a straight line  
359 or >60 km if adults fly along stream corridors. In contrast, adults of resident species that completed  
360 their larval life in Hughes Creek could access many suitable oviposition sites in the same stream  
361 (Macqueen and Downes 2015) with much shorter flight distances. Our results thus show that  
362 commonly used measures of dispersal potential were associated with individuals that, on average, had  
363 to have travelled longer distances. These differences were clear-cut (statistical tests all with  $P$ -values <  
364 0.001) even though the necessity to use closely related species (see Introduction) resulted in fairly  
365 small sample sizes. This is an encouraging outcome because it demonstrates that wing morphology  
366 can be linked to dispersal capacity for some insects, including aquatic insects (see also Kovats et al.  
367 1996). Such evidence is valuable because measuring actual flight distances in nature is difficult for  
368 most insect groups (although more tractable for some, such as the Lepidoptera, Stevens et al. 2010).

369

370 Dispersal events by itinerant species have no demographic outcomes in Hughes Creek and hence the  
371 morphological traits were not associated with effective dispersal in this system. Theoretically, some of  
372 these individuals may continue dispersing to other locations and reproduce successfully. This is the  
373 first study, to our knowledge, to demonstrate a link between itinerancy and dispersal potential. The  
374 implication is that it may be inappropriate to use dispersal traits to make inferences about whether  
375 insect populations are connected demographically, a matter that has concerned some researchers  
376 (Lowe and McPeck 2014), but data to illustrate the problem are scarce. Why do itinerants exist if  
377 individuals may be demographic dead ends? Itinerant individuals may have zero fitness, but in a life

378 history context, some long-distance dispersers may be successful, allowing populations to exploit new  
379 habitats and maintain connectivity within metapopulations. For itinerants, many dispersal events may  
380 be unsuccessful or some individuals may visit multiple habitat patches before oviposition occurs  
381 (Svensson 1998; Conrad et al. 1999). Among aquatic insects at least, itinerancy may be associated  
382 with the rapid colonization of new or restored aquatic habitats (Miller et al. 2010)

383

384 Itinerancy may be more widespread and common than ecologists have appreciated hitherto and it  
385 appears to be common among aquatic insects (e.g. Waringer 1991; McCauley 2006). Within the  
386 Trichoptera, itinerancy is not unique to the family Ecnomidae (of the 68 species in 15 families of  
387 Trichoptera identified in Hughes Creek in 2013-2014, at least 7 species across 4 families were  
388 itinerants (unpublished data)), and itinerancy has been observed in other taxonomically diverse  
389 caddisfly assemblages (Svensson 1974; Sode and Wiberg-Larsen 1993). Itinerancy patterns can be  
390 persistent: for species of *Ecnomus* we observed the same pattern in Hughes Creek over three  
391 consecutive years (the same species classifying as residents or itinerants) and the same pattern  
392 occurred five years earlier in Hughes Creek and a nearby stream (Downes et al. in press). It is unclear  
393 why these itinerant species fail to recruit in this system and this requires a separate investigation, but  
394 we are confident that our samples would have collected their larvae had they been present.

395

396 Flight capability is a function of both wing size and shape so whether itinerants are capable of flying  
397 longer distances than residents depends on the relative contributions of these factors to flight. Size and  
398 shape variables were correlated in for these species of *Ecnomus* and the correlation directions  
399 indicated that increased wing size was generally accompanied by shape changes that also facilitate  
400 long distance flight capability. The magnitudes of interspecific differences were greater for wing size  
401 than shape. For example, comparing wing lengths of the two species with the longest and shortest  
402 wings revealed a 1.3× difference for males, and 1.15× for females. In contrast, differences in  $\hat{r}_2(S)$   
403 were much smaller at 1.015× for males and 1.007× for females. As shown by Weis-Fogh (1973) and  
404 Ellington (1984b), the lift forces of wings increase in proportion to  $R^3$  (the cubic power of wing  
405 length), but increase only linearly with shape parameters. Thus, within the genus *Ecnomus*, small

406 changes in wing length may result in substantial changes in flight capability, relative to changes in  
407 shape parameters of similar magnitude. This may not be true for taxonomically more diverse groups of  
408 caddisflies where wing size and shape may not be correlated, wing shapes may be more diverse, and  
409 where other taxon-specific factors may influence flight capability (Ivanov 1986, 1989, 1990).

410

411 Sexual dimorphism and sex-biased dispersal is common among insects, but the nature of such sex-  
412 biases did not differ between itinerant and resident species in this study. Among aquatic insects,  
413 empirical evidence suggests that females disperse farther than males in some Ephemeroptera (Caudill  
414 2003; Hughes 2007) and some Odonata (Beirinckx et al. 2006), whereas some male Plecoptera  
415 disperse farther than females (Kuusela and Huusko 1996). Based on wing morphology, our results  
416 suggest that female *Ecnomus* may have the potential to travel longer distances than males.

417 Additionally, although females significantly out-numbered the males trapped for some species, sex  
418 ratios in the samples did not differ between resident and itinerant species, as expected if actual  
419 dispersal distances were greater for females. Female-biased samples of caddisflies at light traps occurs  
420 in other species and the possible explanations include sex-specific attraction to UV lights,  
421 reproductive behaviours, habitat use, or simply that females may live longer than males (Svensson  
422 1974; Kovats et al. 1996; Petersen et al. 1999).

423

424 Evidence that a capacity to travel long distances is associated with actual dispersal distances is an  
425 important step forward in assessing the utility of morphological parameters as dispersal traits.

426 However, other species-specific traits or behaviours may simultaneously influence dispersal distances  
427 in diverse ways and may be influenced by diverse selection gradients (Duputié and Massol 2013).

428 Disentangling how various traits interact and the demographic consequences for certain trait  
429 combinations requires further research. For example, for caddisflies (and many other taxa), we do not  
430 know whether traits reflecting flight potential and flight direction are correlated. Many insects,  
431 including some caddisflies, can travel long distances during mating and swarming, but remain within a  
432 relatively small area (Gullefors and Petersson 1993), suggesting that travel and dispersal distances  
433 may not be correlated for some species. Thus morphological traits may suggest strong dispersal



434 potential for some species that actually have low rates of inter-patch movement and various selection  
435 gradients can lead to such behaviourally constrained dispersal (Murrell et al. 2002). Similarly, many  
436 insects travel primarily along stream corridors, whereas other are more likely to fly laterally away  
437 from river channels (Svensson 1974), provided that stream valleys are not deeply incised (Hughes et  
438 al. 1999). It is plausible that itinerants are more likely to disperse laterally away from streams and  
439 have high inter-patch movement rates, whereas species that strongly favour dispersal along river  
440 corridors are more likely to be classified as residents and rarely move between catchments or  
441 discretely different habitat patches. Among the resident species, *E. continentalis* had the strongest  
442 dispersal potential and was abundant throughout the 22 km length of the study stream. In contrast, the  
443 two residents with weaker flight capability, *E. cygnitus* and *E. pansus*, were restricted to shorter  
444 stream lengths. A field experiment also suggested that *E. cygnitus* tends to remain in upstream areas  
445 (Lancaster and Downes 2017). We do not know where larvae of itinerant *Ecnomus* occur in this  
446 landscape, and that requires a separate investigation.

447

448 Overall, our results suggest that morphological traits may be useful in determining the relative  
449 capacity of congeneric species to make inter-patch movements and hence the relative probability that  
450 species have the capacity to change spatial distribution or to colonize new or restored habitat patches.  
451 On their own, however, these morphological traits may mislead about the degree of demographic  
452 connectedness of populations. Stronger inferences may require that morphological parameters are  
453 coupled with other dispersal traits (e.g. flight direction) and with information on recruitment or  
454 reproductive success. Our data show that itinerants are not necessarily rare and may comprise a  
455 consistently high proportion of dispersing individuals. In such cases, dispersal traits coupled with  
456 numbers of individuals sampled in different locations are insufficient to deduce the exact role  
457 dispersal plays in connecting populations. Many studies of aquatic insect metacommunities are based  
458 on analyses of survey data of larvae coupled with putative dispersal traits of adults, and this approach  
459 is clearly problematic if traits do not reflect effective dispersal, i.e. populations that are not  
460 demographically connected (Verberk et al. 2013). It is necessary to collect complementary data that  
461 demonstrate which dispersers are successful at contributing individuals to habitat patches, and which

462 are not. Only then will we be able to disentangle the roles that dispersal plays in metapopulations and  
463 metacommunities.

464

#### 465 **Acknowledgements**

466 We thank the many people who helped with field collections at various times, including Claire  
467 Allison, Wim Bovill, Alena Glaister, Steve Horn, Ashley Macqueen, Bobbi Peckarsky, Jared  
468 Polkinghorne, Bob Smith and Allyson Yarra. We are deeply indebted to Wim Bovill and Alena  
469 Glaister for their stellar assistance with identifications. This project was supported by a Discovery  
470 grant from the Australian Research Council (DP120103145) awarded to JL and BJD. Adult sampling  
471 in 2015 was carried out in conjunction with an NSF Postdoctoral Extension awarded to R. Smith and  
472 hosted by the University of Melbourne.

473

#### 474 **References**

475 Beirinckx K, Van Gossum H, J. Lajeunesse M, R. Forbes M (2006) Sex biases in dispersal and  
476 philopatry: insights from a meta-analysis based on capture–mark–recapture studies of  
477 damselflies. *Oikos* 113:539-547

478 Belyea LR, Lancaster J (1999) Assembly rules within a contingent ecology. *Oikos* 86:402-417

479 Betts CR, Wooton RJ (1988) Wing shape and flight behaviour in butterflies (Lepidoptera:  
480 Papilionoidea and Hesperioidea): A preliminary analysis. *Journal of Experimental Biology*  
481 138:271-288

482 Bilton DT, Freeland JR, Okamura B (2001) Dispersal in freshwater invertebrates: mechanisms and  
483 consequences. *Ann. Rev. Ecol. Syst.* 32:159-181

484 Cartwright DI (1990) The Australian species of *Ecnomus* McLachlan (Trichoptera: Ecnomidae).  
485 *Memoirs of the Museum of Victoria* 51:1-48

486 Cartwright DI (1997) Preliminary guide to the identification of late instar larvae of Australian  
487 Ecnomidae, Philopotamidae and Tasmiiidae (Insecta: Trichoptera). Cooperative Research Centre  
488 for Freshwater Ecology, Albury

489 Caudill CC (2003) Measuring dispersal in a metapopulation using stable isotope enrichment: high  
490 rates of sex-biased dispersal between patches in a mayfly metapopulation. *Oikos* 101:624-630

491 Chessman BC (1986) Dietary studies of aquatic insects from two Victorian rivers. *Aust. J. Mar.*  
492 *Freshwat. Res.* 37:129-146

493 Collier KJ, Smith BJ (1998) Dispersal of adult caddisflies (Trichoptera) into forests alongside three  
494 New Zealand streams. *Hydrobiologia* 361:53-65

495 Conrad KF, Willson KH, Harvey IF, Thomas CJ, Sherratt TN (1999) Dispersal characteristics of  
496 seven odonate species in an agricultural landscape. *Ecography* 22:524-531

497 Downes BJ, Lancaster J (2010) Does dispersal control population densities in advection-dominated  
498 systems? A fresh look at critical assumptions and a direct test. *J. Anim. Ecol.* 79:235-248

499 Downes BJ, Lancaster J, Glaister A, Bovill W (in press) A fresh approach reveals how dispersal  
500 shapes metacommunity structure in a human-altered landscape. *J. Appl. Ecol.*

501 Downes BJ, Lancaster J, Hale R, Glaister A, Bovill W (2011) Plastic and unpredictable responses of  
502 stream invertebrates to leaf pack patches across sandy-bottomed streams. *Mar. Freshwater Res.*  
503 62:394-403

504 Dudley R (2000) *The Biomechanics of Insect Flight: Form, Function, Evolution.* princeton University  
505 Press, Princeton, NJ

506 Duputié A, Massol F (2013) An empiricist's guide to theoretical predictions on the evolution of  
507 dispersal. *Interface Focus* 3:20130028

508 Ellington CP (1984a) The aerodynamics of hovering insect flight. II. Morphological parameters. *Phil.*  
509 *Trans. Roy. Soc. Lond. B* 305:17-40

510 Ellington CP (1984b) The aerodynamics of hovering insect flight. VI. Lift and power requirements.  
511 *Phil. Trans. Roy. Soc. Lond. B* 305:145-181

512 Floreano D, Zufferey J-C, Srinivasan MV, Ellington CP (eds) (2010) *Flying Insects and Robots.*  
513 Springer-Verlag, Heidelberg

514 Gullefors B, Petersson E (1993) Sexual dimorphism in relation to swarming and pair formation  
515 patterns in leptocerid caddisflies (Trichoptera, Leptoceridae). *J. Insect Behav.* 6:563-577

516 Hedrick TL, Combes SA, Miller LA (2015) Recent developments in the study of insect flight. *Can. J.*  
517 *Zool.* 93:925-943

518 Hughes JM (2007) Constraints on recovery: using molecular methods to study connectivity of aquatic  
519 biota in rivers and streams. *Freshwater Biol.* 52:616-631

520 Hughes JM, Mather PB, Sheldon AL, Allendorf FW (1999) Genetic structure of the stonefly,  
521 *Yoraperla brevis*, populations: the extent of gene flow among adjacent montane streams.  
522 *Freshwater Biol.* 41:63-72

523 Humphries P, Brown P, Douglas J, Pickworth A, Strongman R, Hall K, Serafini L (2008) Flow-related  
524 patterns in abundance and composition of the fish fauna of a degraded Australian lowland river.  
525 *Freshwater Biol.* 53:789-813

526 Ivanov VD (1986) Comparative analysis of wing kinematics in caddis flies (Trichoptera).  
527 *Entomological Reviews* 65:60-71

528 Ivanov VD (1989) Action of wing articulations of caddis-flies (Trichoptera) in flight. *Entomological*  
529 *Review* 68:119-129

530 Ivanov VD (1990) Comparative analysis of the aerodynamics of flight of caddisflies (Insecta:  
531 Trichoptera). *Entomological Review* 69:51-66

532 Kovats ZE, Ciborowski JJH, Corkum LD (1996) Inland dispersal of adult aquatic insects. *Freshwater*  
533 *Biol.* 36:265-276

534 Kuusela K, Huusko A (1996) Post-emergence migration of stoneflies (Plecoptera) into the nearby  
535 forest. *Ecol. Entomol.* 21:171-177

536 Lancaster J, Downes BJ (2015) Population densities and density-area relationships in a community  
537 with advective dispersal and variable mosaics of resource patches. *Oecologia* 176:985-996

538 Lancaster J, Downes BJ (2017) A landscape-scale field experiment reveals the importance of dispersal  
539 in a resource-limited metacommunity. *Ecology* 98:565-575

540 Lancaster J, Downes BJ, Arnold A (2011) Lasting effects of maternal behaviour on the distribution of  
541 a dispersive stream insect. *J. Anim. Ecol.* 80:1061-1069

542 Lancaster J, Downes BJ, Glaister A (2009) Interacting environmental gradients, trade-offs and  
543 reversals in the abundance–environment relationships of stream insects: when flow is  
544 unimportant. *Mar. Freshwater Res.* 60:259-270

545 Levin SA, Muller-Landau HC, Nathan R, Chave J (2003) The ecology and evolution of seed dispersal:  
546 A theoretical perspective. *Annu. Rev. Ecol. Evol. S.* 34:575-604

547 Lowe WH, McPeck MA (2014) Is dispersal neutral? *Trends Ecol. Evolut.* 29:444-450

548 Macqueen A, Downes BJ (2015) Large-scale manipulations of oviposition substrata affects egg supply  
549 to populations of some stream-dwelling caddisflies. *Freshwater Biol.* 60:802-812

550 Marchant R (1988) A subsampler for samples of benthic invertebrates. *Bulletin of the Australian*  
551 *Society for Limnology* 12:49-52

552 McCauley SJ (2006) The effects of dispersal and recruitment limitation on community structure of  
553 odonates in artificial ponds. *Ecography* 29:585-595

554 Miller SW, Budy P, Schmidt JC (2010) Quantifying macroinvertebrate responses to in-stream habitat  
555 restoration: Applications of meta-analysis to river restoration. *Restoration Ecology* 18:8-19

556 Morrison CA, Robinson RA, Clark JA, Risley K, Gill JA (2013) Recent population declines in Afro-  
557 Palaearctic migratory birds: the influence of breeding and non-breeding seasons. *Diversity and*  
558 *Distributions* 19:1051-1058

559 Murrell DJ, Travis JMJ, Dytham C (2002) The evolution of dispersal distance in spatially-structured  
560 populations. *Oikos* 97:229-236

561 Neboiss A (1986) *Atlas of Trichoptera of the SW Pacific–Australia region*. Dr W. Junk, Dordrecht,  
562 The Netherlands

563 Outomuro D, Adams DC, Johansson F (2013) Wing shape allometry and aerodynamics in calopteryid  
564 damselflies: a comparative approach. *BMC Evolutionary Biology* 13:118

565 Petersen I, Winterbottom JH, Orton S, Friberg N, Hildrew AG, Speirs DC, Gurney WSC (1999)  
566 Emergence and lateral dispersal of adult Plecoptera and Trichoptera from Broadstone Stream,  
567 UK. *Freshwater Biol.* 42:401-416

568 Rasband WS (1997–2012) *ImageJ*. U.S. National Institutes of Health, Bethesda, Maryland, USA,  
569 <http://imagej.nih.gov/ij>.

570 Ribak G, Pitts ML, Wilkinson GS, Swallow JG (2009) Wing shape, wing size, and sexual dimorphism  
571 in eye-span in stalk-eyed flies (Diopsidae). *Biol. J. Linn. Soc.* 98:860-871

572 Sakai AK, Allendorf FW, Holt JS, Lodge DM, Molofsky J, With KA, Baughman S, Cabin RJ, Cohen  
573 JE, Ellstrand NC, McCauley DE, O'Neil P, Parker IM, Thompson JN, Weller SG (2001) The  
574 population biology of invasive species. *Ann. Rev. Ecol. Syst.* 32:305-332

575 Sakar S (2012) A meta-analysis of the traits affecting dispersal ability in butterflies: can wingspan be  
576 used as a proxy? *J. Anim. Ecol.* 81:174-184

577 Schoener TW, Losos JB, Spiller DA (2005) Island biogeography of populations: An introduced  
578 species transforms survival patterns. *Science* 310:1807-1809

579 Schreiber ESG (1995) Long-term patterns of invertebrate stream drift in an Australina temperate  
580 stream. *Freshwater Biol.* 33:13-25

581 Serrano-Meneses MA, Córdoba-Aguilar A, Azpilicueta-Amorín M, González-Soriano E, Székeley T  
582 (2008) Sexual selection, sexual size dimorphism and Rensch's rule in Odonata. *Journal of*  
583 *Evolutionary Biology* 21:1259-1273

584 Sode A, Wiberg-Larsen P (1993) Dispersal of adult Trichoptera at a Danish forest brook. *Freshwater*  
585 *Biol.* 30:439-446

586 Sokal RR, Rohlf FJ (1981) *Biometry*, 2 edn. Freeman, New York

587 Stevens VM, Turlure C, Baguette M (2010) A meta-analysis of dispersal in butterflies. *Biol. Rev.*  
588 85:625-642

589 Stocks IC (2010) Comparative and functional morphology of wing coupling structures in Trichoptera:  
590 Annulipalpia. *Journal of Morphology* 271:152-168

591 Svensson BW (1974) Population movements of adult Trichoptera in a South Swedish stream. *Oikos*  
592 25:157-175

593 Svensson BW (1998) Local dispersal and its life-history consequences in a rock pool population of a  
594 gyrenid beetle. *Oikos* 82:111-122

595 Verberk WCEP, van Noordwijk CGE, Hildrew AG (2013) Delivering on a promise: integrating  
596 species traits to transform descriptive community ecology. *Freshwater Science* 32:531-547

597 Vittoz P, Engler R (2007) Seed dispersal distances: a typology based on dispersal modes and plant  
598 traits. *Botanica Helvetica* 117:109-124

599 Waringer JA (1991) Phenology and the influence of meteorological parameters on the catching  
600 success of light-trapping for Trichoptera. *Freshwater Biol.* 25:307-319

601 Weis-Fogh T (1973) Quick estimates of flight fitness in hovering animals, including novel  
602 mechanisms for lift production. *Journal of Experimental Biology* 59:169-230

603 Zobel M (1992) Plant species coexistence - the role of historical, evolutionary and ecological factors.  
604 *Oikos* 65:314-320

605

606

607

608  
609  
610  
611  
612  
613

Table 1 In three consecutive years, species relative abundances for adults (A) and larvae (L, 3rd, 4th and 5th instars) along the stream gradient (Site 1 = most upstream; Site 12 = most downstream). Symbols reflect relative abundance at each site: ● >30%, ◐ 10–29%, ○ 1–9%, + <1%. N = number of adults collected / larval density (m<sup>-2</sup>) at each site. Adults were not collected from sites 6, 7, 10 and 11 in 2015 (grey cells).

Year	Site	N	Adults (A)							Larvae (L)									
			<i>E. continentalis</i>	<i>E. pansus</i>	<i>E. cygnitus</i>	<i>E. russellius</i>	<i>E. tillyardi</i>	<i>E. turgidus</i>	<i>E. myallensis</i>	<i>E. continentalis</i>	<i>E. pansus</i>	<i>E. cygnitus</i>	<i>E. russellius</i>	<i>E. tillyardi</i>	<i>E. turgidus</i>	<i>E. myallensis</i>			
2013	1	396/39	●		○	○	●	○		●		◐					+		
	2	395/22	●	+	○	○	●	○		●		●							
	3	632/66	●	+	○	○	◐	+		●		◐							
	4	410/179	●			○	◐	+		●		○							
	5	32/147	●	○						●	○	+							
	6	21/73	●				○			●	○								
	7	10/22	●							●		◐							
	8	105/99	●	○				+		●	○								
	9	870/153	●	○	+	+	+	+		●	○	+							
	10	462/89	●	○	+					●	○	○							
	11	1019/39	●	○		+	+	+		●	○								
	12	396/67	●	○	+	+	+	+		●	○								
2014	1	115/8	●			+	●	○		○		●							
	2	34/11	●			○	●	○		●		●							
	3	86/24	●	○	○	○	●	○		●		◐			+				
	4	644/25	●		+	○	○	○		●		○							
	5	250/20	●	○	○	○	○	○		●	○								
	6	548/30	●	○	○	+	○	○		●									
	7	714/4	●	○	○	+	○	○		●									
	8	1585/23	●	○	+	○	○	○		●									
	9	371/33	●	◐	○	○	+	○		●		○							
	10	256/3	●	◐	+	○	○	○		●									
	11	211/8	●	○	+	+	○	○		●									
	12	265/30	●	◐	+	+	○	○	+	●									
2015	1	125/25	◐				●	○		●		●				+			
	2	387/28	●	○	○	+	●	○		●		●							
	3	223/25	●	+	○	○	◐	◐		●		●							
	4	1953/43	●	+	+	○	◐	○		●		○				+			
	5	2017/87	●	+	+		○	+		●	○								
	6	/20	[Greyed out]							●	◐								
	7	/3	[Greyed out]							●	◐								
	8	286/47	●	○	○		+	○		●									
	9	551/58	●	+	+		+	+		●	○								
	10	/10	[Greyed out]							●	○								
	11	/8	[Greyed out]							●									
	12	744/28	●	○	+	+		+		●									



614 Table 2 Summary of two-way ANOVA testing whether wing shape (aspect ratio,  $\hat{r}_2(S)$ ) and wing  
615 size (span, area) differ between species and sexes, followed by a priori pair-wise  
616 comparisons, within each sex, testing for differences between resident and itinerant species  
617 (R vs I). Aspect ratio,  $\hat{r}_2(S)$  and area were calculated for two coupled wing pairs with N = 5  
618 for each species/sex combination; span for a single coupled wing pair with N = 12 for each  
619 species/sex combination. See Figure 3 for illustration.

620

Metric	Effect	df	MS	F	P
Aspect Ratio, $R^2 = 0.63$	Species	5	0.211	11.0	<0.0001
	Sex	1	0.370	19.2	<0.0001
	Species x Sex	5	0.0043	0.222	0.951
	R vs I Female	1	0.0074	0.384	0.538
	R vs I Male	1	0.0625	3.253	0.078
	Error	48	0.0192		
$\hat{r}_2(S)$ , $R^2 = 0.45$	Species	5	$4.8 \times 10^{-5}$	3.76	0.006
	Sex	1	$1.5 \times 10^{-4}$	12.0	0.001
	Species x Sex	5	$1.3 \times 10^{-5}$	1.03	0.409
	R vs I Female	1	$5.2 \times 10^{-9}$	0.0004	0.983
	R vs I Male	1	$7.8 \times 10^{-8}$	0.006	0.940
	Error	48	$1.3 \times 10^{-5}$		
Span, $R^2 = 0.78$	Species	5	5.10	48.6	<0.001
	Sex	1	20.5	196	<0.001
	Species x Sex	5	0.653	6.22	<0.001
	R vs I Female	1	3.11	29.6	<0.001
	R vs I Male	1	8.27	78.8	<0.001
	Error	132	0.105		
Area, $R^2 = 0.83$	Species	5	129	21.2	<0.001
	Sex	1	612	100	<0.001
	Species x Sex	5	27.9	4.56	0.002
	R vs I Female	1	86.2	14.1	<0.001
	R vs I Male	1	91.0	14.9	<0.001
	Error	48	6.11		

621

622

623 Table 3 Summary of correlation coefficients (Pearson product-moment) between different wing  
624 parameters across all species and sexes. In all tests  $df = 58$  and all tests were statistically  
625 significant at  $P < 0.01$

626

Parameter	$R$	$S$	$AR$
$S$	0.764		
$AR$	0.559	0.495	
$\hat{r}_2(S)$	-0.348	-0.413	-0.555

627

628

629

630 **Figure captions**

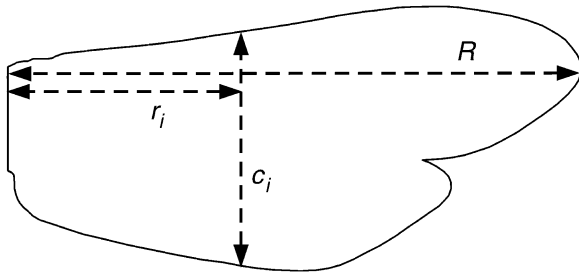
631 **Fig. 1.** Outline of a coupled wing pair showing variables measured and used to measure wing  
632 shape.  $R$  is wing span (forewing length),  $r_i$  is the wing radius or distance from the wing  
633 base to the chord  $c_i$ , which is perpendicular to  $R$  and measured as the distance from the  
634 leading to the trailing edge of the coupled wings

635 **Fig. 2.** Number of females expressed as a proportion of the total adult catch of each species  
636 summed over the 12 sample sites. Bars are means ( $\pm$  SE) of the three years. The dashed  
637 line represents an equal sex ratio. Species grouped according to classification as residents  
638 or itinerants (see text for explanation)

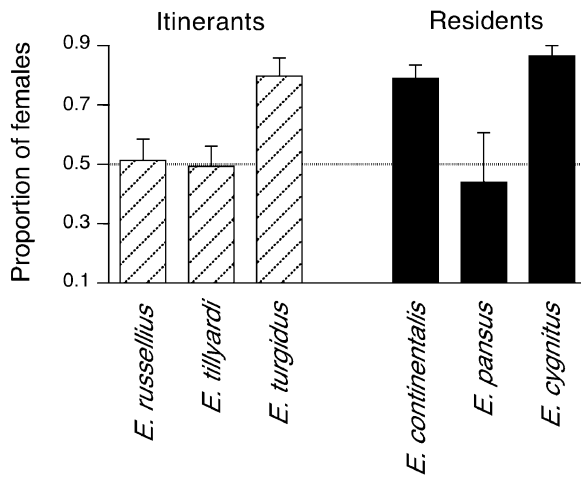
639 **Fig. 3.** Outlines of coupled wings of various species of Trichoptera. (a) Overlain outlines of  
640 males (grey) and females (black) of two species of *Ecnomus*, drawn to scale, to illustrate  
641 differences in shape and size. *Ecnomus rusellius* (solid colours) was the largest species  
642 and has potentially the strongest flight performance within this genus (female AR = 6.16,  
643  $\hat{r}_2(S) = 0.533$ ); *E. cygnitus* (striped colours) was the smallest species and has potentially  
644 the weakest flight performance (male AR = 5.64,  $\hat{r}_2(S) = 0.540$ ). To contrast wing shapes  
645 of *Ecnomus* with other Trichoptera, outlines of coupled wings of males from two  
646 different families (not drawn to scale): (b) *Triplectides ciuskus ciuskus* (Leptoceridae)  
647 (AR = 5.74,  $\hat{r}_2(S) = 0.489$ ) and (c) *Asmicridea edwardsi* (Hydropsychidae) (AR = 3.49,  
648  $\hat{r}_2(S) = 0.509$ )

649 **Fig. 4.** Mean ( $\pm$  SE) (a) wing aspect ratio, (b) the second moment of wing area,  $\hat{r}_2(S)$ , (c) wing  
650 length and (d) area for coupled wing pairs of adult caddisflies of each species grouped  
651 according to sex and whether species were classified as residents or itinerants (see text for  
652 explanation). (a), (b) and (d) were calculated for two coupled wing pairs with  $N = 5$  for  
653 each species/sex combination; (c) measured for a single coupled wing pair with  $N = 12$   
654 for each species/sex combination. See Table 1 for summary of statistical analyses

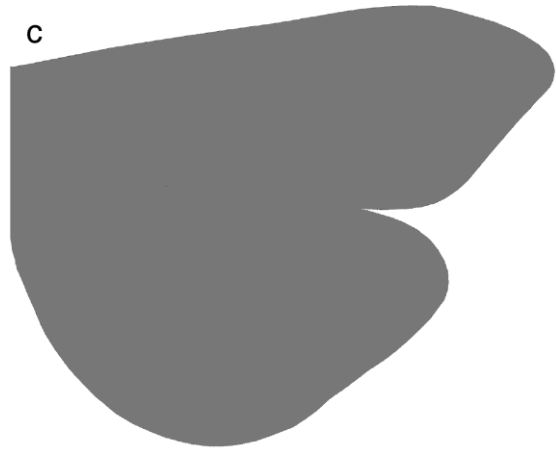
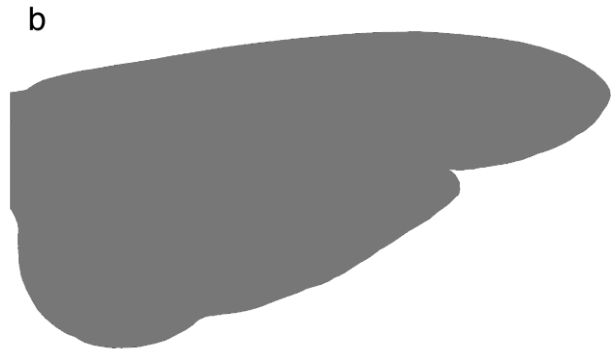
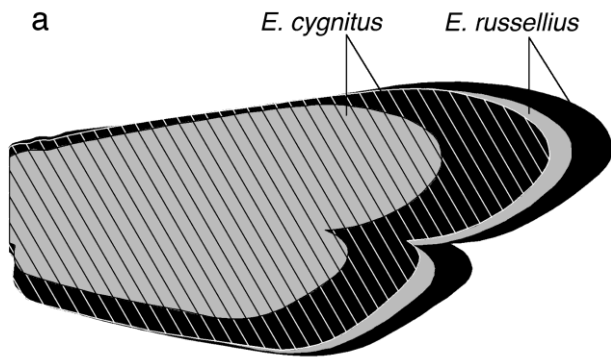
655



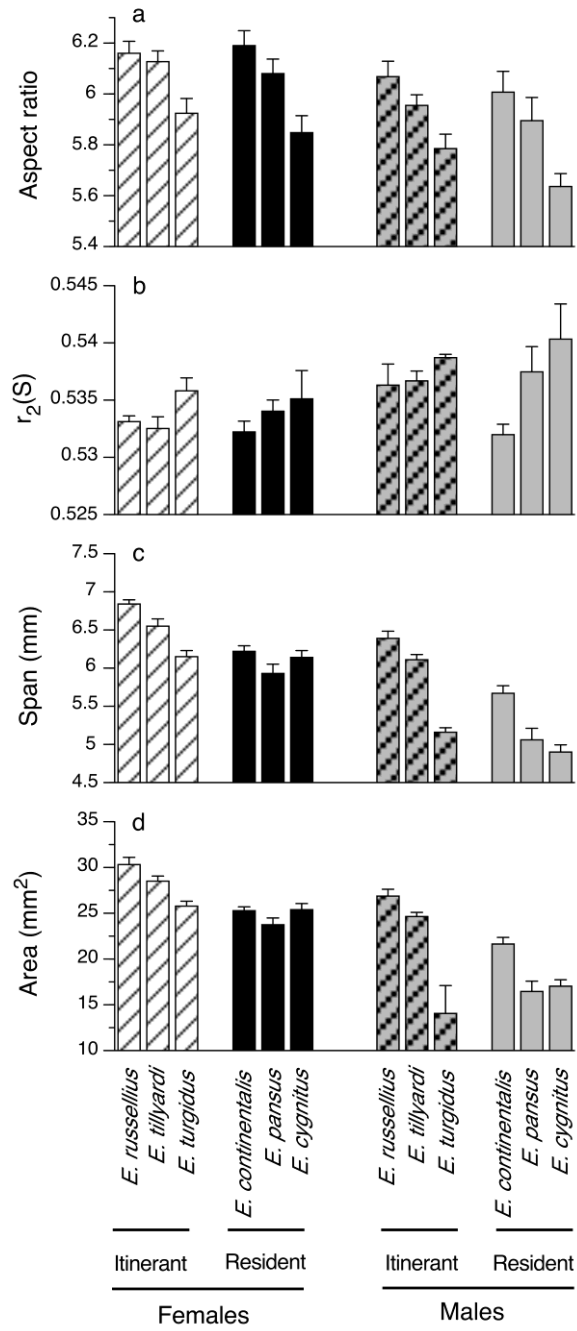
656



657



658





Minerva Access is the Institutional Repository of The University of Melbourne

**Author/s:**

Lancaster, J; Downes, BJ

**Title:**

Dispersal traits may reflect dispersal distances, but dispersers may not connect populations demographically

**Date:**

2017-05-01

**Citation:**

Lancaster, J. & Downes, B. J. (2017). Dispersal traits may reflect dispersal distances, but dispersers may not connect populations demographically. *Oecologia*, 184 (1), pp.171-182. <https://doi.org/10.1007/s00442-017-3856-x>.

**Persistent Link:**

<http://hdl.handle.net/11343/283142>

**File Description:**

Accepted version