

Long range movements by individuals as a vehicle for range expansion in *Calopteryx splendens* (Odonata: Zygoptera)

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Abstract. 1. Flight activity in zygopterans is generally restricted to short-range movements associated with foraging, reproductive activity and escape. Indeed, previous studies have suggested that *Calopteryx* species, including *C. splendens*, are relatively sedentary species, with a low tendency for long distance movements.

2. Recent observations suggest that *C. splendens* is expanding its northern range in the UK; in the northeast the species is now well established in Northumberland and, in the northwest, has recently spread into south-west Scotland. The current study aimed to investigate the mobility and dispersal tendency of *C. splendens* in a well-established breeding population in NE England.

3. A mark-release-recapture study was carried out on a population of *C. splendens* along a section of the River Wharfe, West Yorkshire, UK. 831 adult *C. splendens* were marked uniquely for individual identification in order to monitor the day-to-day, and overall, distance and direction of movement for each individual. Of these 381 were recaptured at least once.

4. The majority of males (85%) and females (88%) moved a distance of 100 m or less and only five of the recaptured individuals (1.3%) moved a minimum distance in excess of 500 m. Although the median distance moved by males was greater than that for females, this was not significant. In addition, there was no significant difference in the number of either males or females moving upstream as opposed to downstream.

5. The results are compared with those from other studies on calopterygid movement. Although most individual *C. splendens* stay within a suggested home range of approximately 300 m, clearly individuals have the potential to cover relatively long distances, and it is these latter movements that play a fundamental role in increasing the range of the species.

INTRODUCTION

Insect movement has been classified into two main types (Danthanarayana, 1986): (1) non-migratory movements involving flights within the habitat or home range. These flights include activities such as foraging, mating, oviposition and movements to and from roosting sites, and (2) migratory movements, which facilitate the colonisation of new habitats and recolonisation of old habitats. These are movements across the wider landscape.

All species exhibit a tendency to move as a means of predator avoidance, food and mate searching, and habitat selection. The distance and duration of movement can vary in relation to the physical condition, age and sex of an individual and in response to environmental factors (Rudd & McEvoy, 1996) such as resource availability, interaction with conspecifics, and physical barriers within the environment (Schutte et al., 1997).

For most odonates, spatial displacement by flight is largely confined to trivial flights (Johnson, 1969) involving relatively brief, short-range, appetitive movements associated with immediate goals such as escape, foraging or reproduction (Corbet, 1999). Mature adults tend to make only short daily movements to nocturnal roosting sites, unless displaced by a storm (Mitchell, 1962) or as a result of territorial disputes (Switzer, 1997a, b).

For species in which the male exhibits territoriality, aggressive behaviour of unpaired males spaces them out along the river margins where they intercept females. In this way interference of copulation and oviposition is reduced, and sperm competition lessened. In areas of high quality oviposition sites, frequent territorial interactions can result in dispersal to previously uninhabited areas (Corbet, 1980). Thus, for *Calopteryx splendens* (Harris), and other species that exhibit territoriality, the majority of small-scale movements are directly related to selection of suitable habitat for territory (and territory defence) and courtship.

For many species of animal only a small proportion of a resident population migrates, and that proportion may change with different environmental cues (Rankin & Burchsted, 1992). Previous studies have suggested that *Calopteryx* species, including *C. splendens*, are relatively sedentary species, with a low tendency for long distance movements (Zahner, 1960; Waage, 1972; Stettmer, 1996; Schutte et al., 1997). More recently, however, there are indications that *C. splendens* is expanding its northern range in the UK (Ward & Mill, 2004). The species is now well established in Northumberland (Jeffries et al., 2005) and has recently been recorded in south-west Scotland (Mearns & Mearns, 2005), there being no previous observations in Scotland. The current study aimed to investi-

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gate the mobility and dispersal tendency of *C. splendens* in a well-established breeding population in NE England.

MATERIAL AND METHODS

The study was conducted over a 28 day period from 24th June to 21st July 2000, along a 1.5 km stretch of the River Wharfe at Newton Kyme, West Yorkshire, England (53°54'5"N, 1°16'57"W; British National Grid Reference SE245455). The study area was divided into 20 continuous stretches of 75 m along the riverbank. Each one of the 20 areas of riverbank was assigned a specific letter, for ease of identifying location when recording marked insects. Wooden marker posts were placed every 10 m along the length of the riverbank for reference when recording the location of all captured and recaptured damselflies.

Adult *C. splendens* were captured on 18 out of the 28 days; the time between searches varying from 1 to 3 days according to weather conditions. The sampling period reflected the activity of the damselflies, and was carried out between the hours of 0900 and 1600 (GMT). An insect sweep net was used to capture adult *C. splendens*, which were uniquely marked on the left forewing using a fine indelible pen. On each sampling occasion, individuals without a mark were captured and marked accordingly. Upon initial capture, the sex of the individual and the assigned unique identification number were recorded. On all initial and subsequent recaptures, the location to the nearest metre was estimated. All individuals were released at, or close to, the point of capture. When possible, "recaptures" were made with the use of binoculars to avoid repeated, unnecessary handling of individuals.

The distance and direction of movement were recorded for each individual on each day of recapture. This gave both the total distances moved, and the overall direction of movement.

RESULTS

831 individuals (403 males and 428 females) were marked, 381 (203 males and 178 females) of which were subsequently recaptured. Of these, approximately half were recaptured only once (52% males and 62% females), with a progressive decrease in the number of multiple recaptures.

Overall movement

The number of recaptures would be affected by mortality and permanent emigration and the recorded distances were considered to be minimum distances moved. Considering those individuals recaptured at least once, relatively few (15% males and 12% females) moved distances of over 100 m (Fig. 1A) and only five (1.3%) moved over 500 m. Three of the latter were males, one of which moved at least 738 m; the furthest recorded distance moved by a female was 556 m. It is quite possible that some individuals moved greater distances. However, any individual that moved beyond the confines of the study area would clearly not be recorded.

The majority of males (85%) and females (88%) moved a distance of 100 m or less (Fig. 1A). Furthermore, 70 % of males and 74 % of females did not exceed movement distances of 50 m (Fig. 1B), and 24% of males and 26% of females did not move any further than 5 m from the area of their initial capture (Fig. 1C); indeed a small proportion of the population, 4% each of the males and

TABLE 1. Distance moved (m) between June 24th and July 21st 2000 by adult *C. splendens*, at Newton Kyme on the River Wharfe.

Sex	n	Median distance (m)	St. deviation	Range (m)
Males	203	21	105.44	0–738
Females	178	18	86.17	0–556

females, did not move at all between consecutive sampling occasions (Fig. 1C).

On average males moved a minimum distance of 1.17 m/day; females a minimum distance of 1.00 m/day. The median distance moved by males was greater than that for females (Table 1), but this was not significant (Mann-Whitney $U = 16246.5$, $P = 0.40$).

It should be noted that the distances given are linear distances along the river, which had a considerable meander. It is possible that some individuals crossed the intervening meadow to reach their destination but most individuals moved small distances from day to day, which is commensurate with following the course of the river. Furthermore, few individuals were seen over the meadow away from the vicinity of the river.

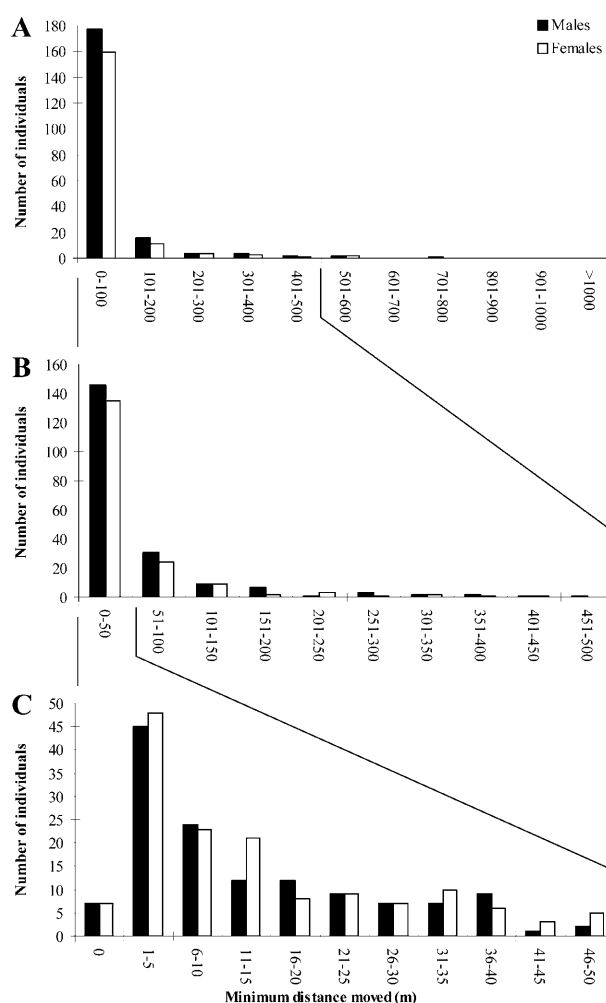


Fig. 1. Minimum distances moved (m) by adult male and female *C. splendens*, when distances are measured at (A) 100 m, (B) 50 m, and (C) 5 m intervals.

Movement patterns

There was no significant difference in the number of males ($\chi^2 = 0.57$, d.f. = 1, $P = 0.39$) or the number of females ($\chi^2 = 0.23$, d.f. = 1, $P = 0.55$) moving upstream as opposed to downstream and this also applied to the subset of those that moved longer distances. Furthermore, of the 203 males and 178 females which were recaptured at least once, 58% of the males and 61% of the females were captured within 10 m of the previous point of capture and were assumed to show no inclination to move in either direction.

Four distinct movement patterns were identified from those individuals (43 males and 37 females) that were recaptured at least three times. Of these animals, 35% of males and 38% of females remained within 10 m of their initial point of capture (IPC). A return to within 10 m of the IPC, following movements of between 20 m to 80 m away, was observed in 9% of the males and 11% of the females, whilst 22% of males and 24% of females exhibited a movement away from the IPC, then settled in a new area. These movements were between 20 m to 100 m away from the IPC, although one male flew 361 m before settling in a new area. Of those individuals that showed progressive movement away from the IPC, 34% of males and 27% of females exhibited this pattern of movement. Distances covered were between 40 m and 600 m.

DISCUSSION

Over the four week period of the current study 72% of individual *C. splendens* moved less than 50 m, and 87% less than 100 m, from their release site. Fuhrmann (1990) recorded 70% less than 30 m and 90% less than 200 m; Stettmer (1996) found that 86% dispersed less than 150 m and Schutte et al. (1997) 58% less than 100 m. Zahner (1960) found that most *C. splendens* and *C. virgo* individuals moved between 10 m to 200 m, with only 3% moving distances greater than 400 m. *C. maculata* shows a similar movement pattern (Waage, 1972). At the other extreme, in the current study, only 1.3% were found to move distances greater than 500 m with the furthest recorded distances being 738 m for males and 556 m for females. In a comparable study Schutte et al. (1997) found 2.2% exceeding a distance of 1000 m and recorded a maximum of 1725 m for males and 1475 m for females but their study area extended 2000 m compared with the 1500 m of the current study. Stettmer (1996) recorded 7.7% exceeding 300 m. Conrad & Herman (1990) found that female *Calopteryx aequabilis* were the more mobile, the males moving very little after establishing a territory. Waage (1972) found that, although females of *Calopteryx maculata* “were significantly more mobile than males, as expressed by their median movement”, “the mean distance moved by males was greater than that for females, reflecting a small number of extreme movements by some males”.

For species that exhibit territoriality, it may be expected that increased population densities would initiate increased migration, especially by males some of whom may have to move considerable distances before locating

a suitable vacant territory, whereas only a proportion of the females will be at water at any one time (e.g. Bennett & Mill, 1995). Females do not compete for territory sites (Waage, 1972) and would not normally “have to move out of an area containing numerous oviposition sites to acquire mates or places to oviposit” (Waage, 1972). However, in *Pyrrhosoma nymphula*, Bennett & Mill (1995) found that females tended to move greater distances than males and suggested that this may be because males tended to return to the same area each day whereas females have a greater opportunity to wander as they do not visit water every day.

Of the individuals that conformed to one of the movement patterns described in the current study, the majority of males and females tended to remain within a few metres of their initial point of capture. Switzer (1997a, b) found that movement in the territorial damselfly, *Perithemis tenera*, was controlled by site fidelity, individuals returning to, or remaining at, a previously occupied location where breeding success was high; most moves occurring within a day were the result of territory evictions by other males. However, an increase in population density may reduce the number of territory holding males rather than increase dispersal rates. Thus Zahner (1960) reported the occurrence of non-territorial *C. splendens* at population densities between 30 and 60 males per 10 m of bank. A similar situation occurs in *C. virgo* (Pajunen, 1966), *C. maculata* (Waage, 1972) and *Pyrrhosoma nymphula* (P. Mill, pers. obs.). In the current study, the highest male density recorded in any one area was 35 per 10 m of river bank (Ward & Mill, 2005). An increase in the numbers of non-territorial males and decreases in territory size and territorial stability have been correlated with an increase in population density in *C. splendens* and *C. virgo* (Zahner, 1960). Michiels & Dhondt (1991) found that escape flights by male *Sympetrum danae* occurred more often at lower densities than at higher densities, thus suggesting that if the likelihood of encountering a conspecific is low, an individual male will move away from the current site. Similarly, Zahner (1960) found that the attachment of *C. splendens* to a certain territory was reduced in the absence of conspecifics.

For both sexes, few individuals returned to the location of their initial capture, once they had exhibited direct movement away from the area. Consideration of the possible reasons for migration from an area may help to explain this pattern of movement. A habitat may be rendered unsuitable for some individuals for a variety of reasons. Although increased population density is tolerated by the population through behavioural changes (Waage, 1972), serious over-crowding would undoubtedly result in decreased relative resource availability, and thus increased migration. Additionally, disturbance as a result of anthropogenic influence, such as anglers disturbing bank-side vegetation (L. Ward, pers. obs.) and cattle disturbance (Schutte et al., 1997; Ward & Mill, 2005) also incite increased movement. Thus, it is understandable that movement away from an unsuitable habitat would rarely result in a return to the same location. The long distance

movement of a few individuals from a population can ultimately lead to the colonisation of previously unoccupied areas (Kiauta, 1963; Stettmer, 1996). Thus, *C. splendens* has the potential to cover relatively long distances, and it is these movements by a small number of individuals that play a fundamental role in increasing the range of a species.

The current study failed to reveal any significant bias in movements upstream as opposed to downstream, for males or females. Similarly, Garrison (1978) found that stream flow had no deterministic effect on the movements of adult *Enallagma cyathigerum* and *Argia vivida*. Schutte et al. (1997) found that of 17 *C. splendens* individuals that moved more than 1000 m, 11 flew upstream and 6 flew downstream. However, a Chi² test performed on their data revealed that this was not significant (Chi² = 0.94, d.f. = 1, *P* = 0.23). Whilst the aerial stages of many aquatic insects exhibit flight directed upstream (Allan, 1995), these are most notably species from invertebrate orders that largely compose the “drift” fauna, namely the Ephemeroptera, Plecoptera and Trichoptera (Madsen et al., 1973; Svensson, 1974; Müller, 1982; Peckarsky et al., 2000). Odonates are not significant components of the larval drift fauna (D. Dudgeon, pers. comm.); thus upstream movement of ovipositing females is probably not necessary as a compensatory colonisation mechanism. However, Higashi & Ueda (1982) noted that teneral of *Calopteryx cornelia* had a tendency to move upstream. Also Beukema (2002) observed upstream biased movement in a population of *Calopteryx haemorrhoidalis* on a small stream in north-eastern Spain. Emergence was reported only from the lower reaches of the stream, and was explained by larval drift due to strong currents regularly depleting the upper section of the stream. Larval *C. splendens* are known to be swept downstream at flow rates of 0.77 m s⁻¹ or more (Dorier & Vaillant, 1954). Thus for Odonata, “accidental” larval drift probably occurs as a result of dislodgement, as opposed to the active drifting shown by ephemeropteran and trichopteran larvae.

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