

# Changing distribution patterns along a stream in adults of *Calopteryx haemorrhoidalis* (Odonata: Calopterygidae): a case of larval-drift compensation?

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Received 11 April 2001; revised 23 August 2001; accepted 05 September 2001.

Key words: Odonata, dragonfly, damselfly, *Calopteryx*, along-stream distribution, upstream movements, drift compensation, adult life stages.

## Abstract

The distribution of an isolated population of adult *Calopteryx haemorrhoidalis* was studied along a small stream in NE Spain, during two-week or three-week summer periods over five years. Distribution patterns differed consistently between age groups. Reproductive activities took place along the entire stream, whereas the presence of teneral and older immature individuals was restricted to the lower reaches of the stream. It is concluded that emergence took place only in the lower reaches and that this can be explained by larval drift due to strong currents regularly depleting the upper half of the stream.

Recovery of individually marked teneral specimens indicated that immature individuals remained in the area around the lower reaches, during roughly the first week of their adult life. During the following week, when they had attained mature wing coloration but did not yet show reproductive activities, they moved for long distances. This was particularly true for newly matured males, where the distance between two successive encounters could amount to hundreds of meters. By far the greatest proportion of these moves was upstream. Movement in later life stages, i.e. during the reproductive part of their life, was infrequent, much shorter and less consistently directed, though generally more often upstream than downstream. Once the males defended a territory, they hardly moved anymore. Territories were spread more evenly along the stream at high rather than at low overall densities. It is concluded that territorial behaviour contributed to a more even distribution of mature males and that an inborn tendency to fly upstream is not a prerequisite for the observed upstream-biased dispersal during adult life.

## Introduction

Substantial downward migration by larval drift is a common phenomenon in stream-dwelling aquatic insects, particularly during periods of high current velocity (Brittain &

Eikeland 1988; Tockner & Waringer 1997). To maintain high abundance in upstream stretches, populations experiencing serious larval drift may express some compensatory mechanism, such as a better survival of larvae in upstream areas and/or a net upward movement of either the larvae (examples in Söderström 1987) or of a more mobile adult stage (e.g. Müller 1982; Hershey et al. 1993) or of both (e.g. Turner & Williams 2000). Though compensatory upward dispersal may not be an absolutely necessary attribute of populations subject to larval drift (Anholt 1995), it will contribute to population size and persistence (Kopp et al. 2001) and it certainly is the most obvious and effective way to compensate for losses of larvae in upstream areas. Although net upstream movements in adult aquatic insects have often been recorded, it is questionable whether such dispersal generally results from directed upstream migration or from random movements.

Corbet (1999: 646) lists observations on differential distribution of adults and larvae and on upstream movements of adults in rheophilic Odonata species. Although there are some records in Odonata of a greater prevalence of eggs and early larvae upstream as compared to older life stages, and more upstream than downstream directed movements in adults (see also the more complete enumeration on such observations in Calopterygidae in the Discussion), the present evidence for compensatory upstream migration in adult zygopterans should be characterized as largely anecdotal. Therefore, there is some need for a more detailed study dealing with both distribution and movement of adults along a stream in relation to current direction and population density.

Among the Zygoptera, Calopterygidae are typically rheophilic (Corbet 1999: 589) with larvae spending generally almost a full year in flowing waters (Corbet 1999: 218) and thus vulnerable to larval drift. Calopterygids are very suitable for studies of adult movements, because the individuals can be easily caught to be marked and their restricted movements and lack of shyness make it easy to follow their movements precisely.

Two hypotheses are stated: (1) Assuming that the distribution of teneral individuals reliably reflects that of emergence sites (because just emerged individuals cannot fly any long distances), such tenerals should be encountered mainly along the downstream part of a stream if larval drift decisively affects larval distribution. If the entire stream is important for reproductive activities, such as oviposition and territory defense, mature adults should be distributed more evenly along the stream than the tenerals and therefore (2) there should be more and/or longer upstream than downstream movements during an early part of adult life.

Evidence to evaluate these hypotheses was obtained by a study of the distribution patterns of the successive adult life stages and of their along-stream movements in a small and isolated population of *Calopteryx haemorrhoidalis* (Vander Linden) in northeastern Spain. By individually marking immature and mature adults and by daily surveying the stream to note their movements after marking, I tried to assess the distribution and movements of the various age groups and in particular to find out how far they moved, which direction dominated in their movements, and at which period in the adult life such movements predominantly took place.

## Methods

### *Study area*

The population of *Calopteryx haemorrhoidalis* studied, lived along a small stream in the foothills of the eastern Pyrenees in Spain, a few km north of the village of Montagut, between the towns of Besalut and Olot in the province of Girona. The stream is called Torrente del Estanyol and its location is indicated on a map in Wasscher (1996). The section of the stream that was regularly surveyed extended from a cascade close to the source to one about 650 m downstream, where the stream empties itself into a broader valley. Since this rocky valley lacked almost any vegetation and dried up in the course of most summers, it was unsuitable to accommodate *Calopteryx* territories; during some tens of surveys extending to this area, only occasionally a single mature male was observed there. Therefore, the studied adult population along this 650-m stretch appeared to be isolated from suitable neighbouring habitats. These were more than 1 km away and separated by dry woodland and rocks. Although it is known that adults of calopterygids can move over distances of more than 1 km (Stettmer 1995, 1996), results of mark-recapture studies (Beukema 2002) for the present population of *C. haemorrhoidalis* indicated such high daily survival rates (no less than 94% in all life stages and in both sexes) that emigration could not play any significant role in this population.

In summer, the width of the stream locally varied between 0.3 and 5 m, its depth between 0.1 and 1 m, but after heavy rain the water level rose to 1 m higher as judged from debris washed up in the shrubs. Year-to-year changes in the distribution of the debris indicated that high water levels had occurred at least once per year. Sometimes the currents had been so strong that trees were dislodged. The stream bottom was chalky with numerous ridges, slowing down the current speed and creating numerous pools of highly variable size. The borders were mostly wooded with tall trees and shrubs along most of the 650-m stretch, but sunny spots were numerous on and along the water. However, most of the total water surface was in the shade more than half of the day, leaving only a limited number of suitable areas for territories. Water temperature in the June-August period generally ranged from 14°C at the source and in deep pools to 17°C at shallow stretches downstream, but it occasionally rose to over 20°C at the lower reaches. Air temperatures were more variable and rose on sunny summer days to values between 20 and 30°C. However, on about 10% of the days the sky remained overcast during (almost) the entire day and few (if any) *C. haemorrhoidalis* appeared near the water on such days. As judged from their movements during bright spells, they remained in the crowns of the trees during bad weather.

To describe the distribution of the various age groups and sexes of *C. haemorrhoidalis*, the stream was divided into eight sections each of about 80 m, section 1 being the most upstream part and section 8 the most downstream part. The sections differed in relevant environmental characteristics such as the proportion of the water surface area that was sunlit at any time of the day (sections 1, 3, and 4 were relatively dark).

### Observations

As many males as possible and also several females were caught by gentle netting. They were marked by a unique combination of white and/or red spots on the outer sides of the wings or on the upper side of the body. White correction fluid and red nail varnish were applied to make these spots. The present investigations were part of a broader mark-recapture study investigating daily survival of various adult age groups and site fidelity of individuals of different sex and age. Extra mortality on the day of catching and marking was rather low, roughly twice the average mortality of 0.06 per day on later days (Beukema 2002). The location and colour of distinguishing marks, the catching place, the sex and a rough estimate of age were noted. An individual was described as 'immature' if it did not yet show the full mature wing coloration. If, in addition, the wings were still soft, it was noted as 'teneral'. To follow maturation in detail, I tried to catch males marked at an immature state, at resighting, to inspect the coloration of the spot at the end of the abdomen, which gradually changed from whitish to bright rose-red at maturation. I encountered marked immature individuals once per two or three days, however I often failed to catch them. Therefore wing coloration was the criterion generally used to assess the end of the immature state. This was visible from several meters distance, and it changed about one week after the teneral state to a colour indistinguishable from the mature coloration. However, as noted from individuals that I successfully caught, there was roughly one more week before the full red colour of the abdominal spot developed and the male established a permanent territory. Thus an extra stage was discerned between 'immature' and 'mature'. Males were called 'maturing' during the first week they showed mature-like wing coloration.

After about one minute to allow the paint to dry, a marked individual was released at the same place, whereupon it usually flew up into the trees. The numbers of marked individuals and the periods of observation in 1992-1993 and 1996-1998 are listed in Table 1; observations made in 1991 were omitted because only part of the stream was surveyed in that year; observations for 1994 were omitted because of extremely low water levels forcing all Zygoptera to a restricted part of the stream. In most years, nearly all marked individuals already showed mature wing coloration at marking, except for the 1997 season, when also large numbers of immatures coloured specimens could be marked (including several tenerals). In the other years, the emergence season probably had already come (almost) to a close at the time the observation period began.

The part of the population that was present near the water was surveyed once or twice daily during periods of two to three weeks, interrupted by only a few days of inclement weather, in each of the five years, as listed in Table 1. Highest numbers of *C. haemorrhoidalis* were present along the stream between 11:00 h and 17:00 h (local time). The survey track was followed in the stream, nearly entirely, by wading. Locations at marking and at all subsequent encounters (called resightings) were noted with a precision of one to a few meters, relative to characteristic trees and other landmarks indicated on a map. The marks were large enough to allow recognition from a distance of several meters. In working out the detailed data, a displacement was counted as a real move only if the individual had moved at least 10 m relative to the site of the preceding observation. The reason for the choice of this rather large distance

is that territory diameters could amount to more than 5 m, depending on the differential locations of the sunny parts of the stream in the morning and afternoon hours.

Because it proved difficult to find sufficient numbers of the small and inconspicuous exuviae, the location of emergence sites had to be assessed indirectly, viz from the sites where soft-winged teneral were encountered. No attempts were made to collect larvae, because it was not feasible to assess their densities in a quantitative way due to the heterogeneous character of the stream bottom (particularly because of the numerous and irregular chalk ridges).

Table 1. *Calopteryx haemorrhoidalis* — observation periods in five years, total numbers of mature and immature males and females marked in these periods, and proportion (%) of these numbers that were caught (at marking) in the upstream half of the studied area. Significance levels ( $\chi^2$  test with absolute numbers) for differences in upstream/downstream distribution: difference mature/immature males,  $p < 0.001$ ; mature/immature females,  $p < 0.05$ ; mature females/immature males,  $p < 0.01$ .

Year	Period of observation	Numbers marked				Upstream percentage			
		mature		immature		mature		immature	
		male	female	male	female	male	female	male	female
1992	13 vii-27 vii	31	4	0	0	39	50	-	-
1993	14 vii-02 viii	147	35	3	0	41	34	0	-
1996	19 vi-07 vii	102	27	2	0	42	44	0	-
1997	06 vi-25 vi	85	31	26	10	35	29	4	0
1998	12 vi-22 vi	8	9	1	0	25	33	100	-
Totals		373	106	32	10	40	36	6	0

## Results

### *Differential distribution of immature and mature individuals*

During the surveys along the stream, immature *Calopteryx haemorrhoidalis* were observed almost exclusively along the three most downstream sections (Fig. 1). The 42 immature individuals marked included 14 teneral individuals, all resting at short distances from the water surface. Immature individuals with hardened wings were also frequently observed up to several meters away from the stream, but exclusively near the lower half of the surveyed stream. Occasionally an immature individual was seen at longer distances (some tens of meters) from the stream, but again only along the lower half of the stream.

Mature individuals were observed in large numbers in seven sections and were rare only in the one most upstream section (Fig. 1). Males and females showed a very similar distribution; note the common peaks in sections 2 and 7, as opposed to the common lows in sections 1, 3, and 4. The locations of the territories of the reproductive males showed a similar distribution pattern (Fig. 1). The standard errors shown with the solid points in Figure 1 were mostly small, indicating that the distribution patterns in the various groups of mature animals hardly differed between the three years that had high population densities. In each of these three years, the mean distance of the territories to the cascade near the source amounted to  $355 \pm 18$  (mean  $\pm$  s.e., in m),  $327 \pm 20$ , and  $337 \pm 22$  in the years 1993 ( $n = 96$ ), 1996 ( $n = 83$ ), and 1997 ( $n = 53$ ), respectively. The differences between the years were non-significant ( $p > 0.1$ , pair-wise applied t-tests). Note that these average distances were close to halfway down the stream (i.e. 325 m from the source cascade).

Some sections of the stream were significantly preferred (t-tests of pair-wise compared numbers) to others in all years. The preferred sections contained relatively large sunny areas with suitable oviposition sites, as opposed to the mostly "dark" sections 1, 3, and 4.

The restriction of the immature individuals to the lower reaches of the stream was almost complete: 94% of the 32 immature males and 100% of the 10 immature females were first observed and marked in the lower sections 5-8. In the 373 males and 106 females that were mature at marking these proportions were 60 and 64%, respectively (Table 1). The statistical significance of the differences in distribution between the age groups and sexes was tested using contingency tables. Because this test demands that expected numbers per cell exceed 5, numbers found in adjacent sections of the stream had to be added in some cases. All sections could be used separately in the comparison of mature males and females. The distribution of these groups did not differ significantly ( $p \approx 0.5$ ,  $\nu = 7$ ). To compare the distributions of all mature with all immature individuals, numbers in sections 1 + 2, 3 + 4, 5 + 6 and 7 + 8 had to be used, yielding a high  $\chi^2$  value of 25.6 at  $\nu = 3$  ( $p < 0.001$ ). To compare the distributions of teneral and mature individuals, the numbers in sections 1 + 2 + 3 + 4 and those in sections 5 + 6 + 7 + 8 had to be combined, yielding a  $\chi^2$  value of 8.8 at  $\nu = 1$  ( $p < 0.01$ ). In the same way, a non-significant difference between tenerals and older immature individuals was found ( $\chi^2 = 1.0$  at  $\nu = 1$ ). Thus, only the distribution along the stream of the two major age categories (immature and mature) differed significantly, whereas within these groups (teneral or not, male or female) differences were non-significant.

The distribution of the territories along the stream was far from even (Fig. 1). In the various years, the coefficient of variation of the mean number of territories per section varied from 0.70 to 1.54. The decline of these coefficients with increasing density (Fig. 2) indicates that territories were spread more evenly along the stream at high rather than at low densities.

The proportion of all established territories that was located along the upper half of the stream hardly varied from year to year, viz 33-45%, and showed no consistent relationship with population density or date. The possible relationship with the season was tested for the three high-density years by counting the number of territories per

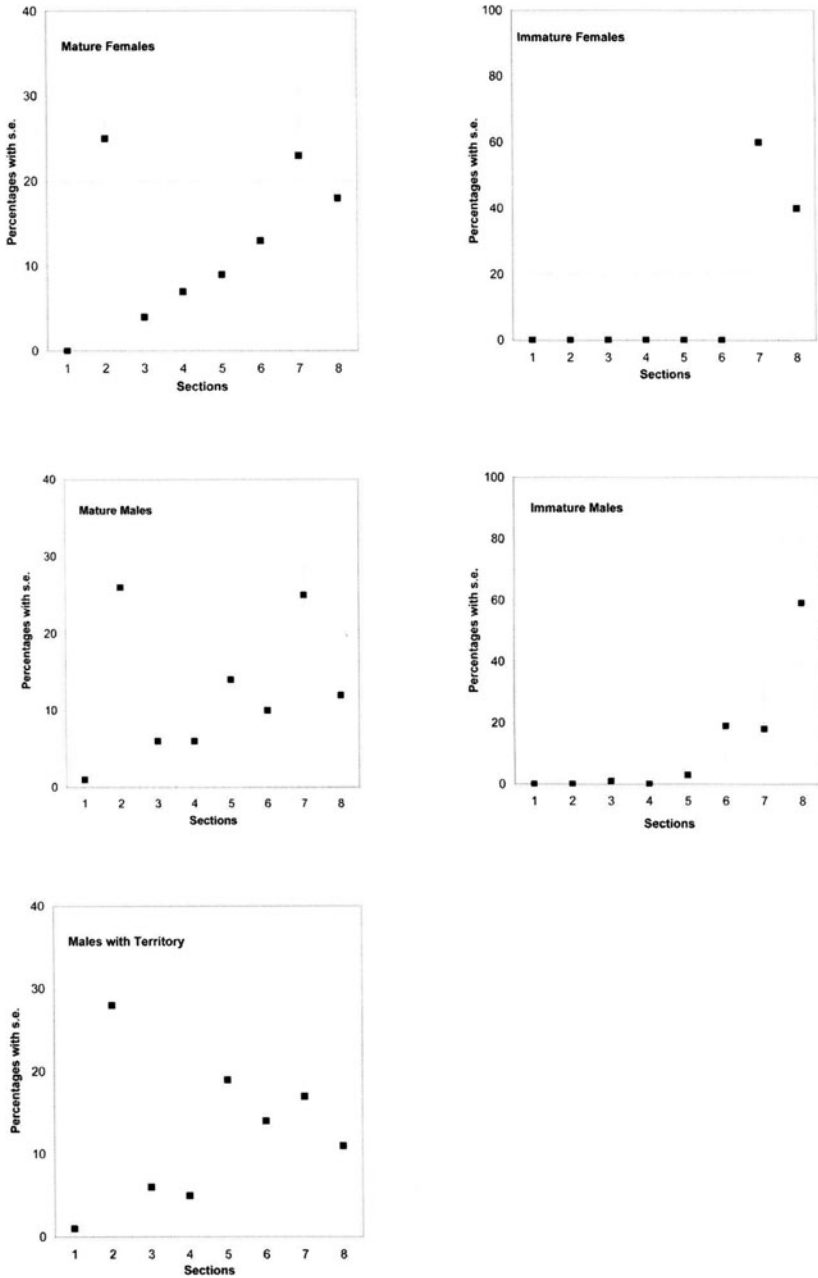


Figure 1. *Calopteryx haemorrhoidalis* — distribution of different groups along the eight successive sections of the stream (1 = most upstream to 8 = most downstream section of the area studied), expressed as mean percentage of total at each section with 1 s.e.;  $n = 3$ , viz the years 1993, 1996 and 1997 when the species were numerous (compare Table 1). No s.e. indicated for immature females, because this group was present only in 1997.

section within fortnightly periods. The percentages of the territories located along the upper half of the stream were 35% ( $n = 46$ ) in the first half of June, 40% ( $n = 109$ ) in the second half of June, 42% ( $n = 73$ ) in the first half of July, and 38% ( $n = 89$ ) in the second half of July. No clear trend is apparent, nor were the differences statistically significant ( $\chi^2$  tests with the indicated numbers and  $\nu = 1$ ).

### *Movements of different age groups*

The age groups differed strongly in their tendencies to move. This was particularly clear in males. Territorial males were generally seen day after day at the same site and were rarely encountered at another place, viz at only 12-14% of the observation days (see Table 2). On the other hand, as long as males had not yet established a territory (the groups of 'maturing' and 'non-territorial' in Table 2) they were seen at places that usually, viz 82-86% of the observations, differed from day to day. Immature-coloured males and all age groups of females were intermediate in their mobility (Table 2).

The mean total net distances – i.e. between first and last encounter with an individual within a certain life stage – were small, viz some tens of m or less, in nearly all groups, but were an order of magnitude larger (Table 2) in the group of maturing males. Thus this particular group of maturing males was exceptional in showing more frequent moves over much longer distances than any other group. The group of mature non-territorial males also moved frequently, though on average over smaller net distances. This was a less homogeneous group in terms of age, because it contained all fully mature males that happened to stay only a short time at the marking site and thus included both pre- and post-territorial males. In females, the group of maturing individuals likewise showed relatively long distances covered, as compared to other groups of females. Unfortunately, the numbers of females marked at an immature stage were too small to judge the statistical significance of their data.

The prevailing directions of the moves (Table 2) were more often upstream than downstream in most age groups of the males. Statistically significant differences were found only in the group of maturing males (sign test,  $p < 0.01$  and  $< 0.05$  for all movements and net displacements, respectively). For the entire group of mature males (totals of three subgroups of Table 2), the difference in "all moves" (280 upstream versus 234 downstream) was only just significant ( $p < 0.05$ , sign test). Thus the group of maturing males stood out in particular, demonstrating a clear preference for moving upstream. In females, a similar tendency can be seen in maturing individuals, but in numbers too low to show statistical significance.

## **Discussion**

A differential distribution of immature and mature *Calopteryx haemorrhoidalis* was observed in both sexes (Table 1, Fig. 1): mature individuals occurred along the entire stream, whereas immature specimens were restricted to its lower reaches. Because teneral, which could not have moved for any long distances between emergence



Table 2. *Calopteryx haemorrhoidalis* — a summary of data on along-stream movements, separately for five groups of males and three groups of females, viz immature individuals showing non-mature wing colouration, maturing individuals of known age, i.e. wing colours still immature  $\leq 1$  week before, and mature individuals of unknown age, but with mature wing and abdominal-spot colouration at marking. The group of mature males divided into: non-territorial (not staying at the marking site at subsequent days) and territorial (individuals with either a territory already at marking = 'immediate', or observed to establish a territory after a non-territorial period = 'later'). Data are given for:

- an index of mobility, viz the percentage of all days of observation of males of the group showing a net move of  $\geq 10$  m;  $n$  = numbers of male-days. Differences between percentages were significant ( $p < 0.01$ ,  $\chi^2$  tests with absolute numbers) if not followed by the same character (a, b, or c).
- mean net distances per individual between sites of marking and last resight during subsequent surveys (in m), separately for all individuals and for moving individuals only;  $n$  = numbers of individuals; the bold figures differed significantly ( $p < 0.01$ ) from all other figures in the same column (pair-wise t-tests).
- direction of all moves ( $\geq 10$  m), expressed as numbers of day-to-day moves either upstream (+) or downstream (–) and direction of net displacements during entire period of observation of each individual, expressed as numbers of individuals showing either (net +) or (net –) moves. Significant differences indicated by asterisks.

Group	Mobility (% of all obs. days showing net moves)			Mean net distance (m)				Direction			
				All		moving		all		net	
	%	$n$		individuals		individuals		moves		displacements	
				m	$n$	m	$n$	$n$	$n$	$n$	$n$
<b>Males</b>											
immature	39	38	a	+11	21	+24	10	11	4	7	2
maturing	82	44	b	<b>+155</b>	15	<b>+166</b>	14	29*	7	12**	2
mature:											
non-terr.	86	469	b	+20	162	+21	153	217	185	80	69
terr., immediate	14	484	c	+12	116	+41	34	43	26	19	11
terr., later	12	347	c	+2	78	+5	30	20	23	14	15
<b>Females</b>											
immature	29	7	a, c	–8	6	–25	2	0	2	0	2
maturing	25	24	a, c	+47	6	+93	3	5	1	2	1
mature	45	309	a	0	83	0	63	69	70	27	33

\*  $p < 0.01$ ; sign test

\*\*  $p < 0.05$ ; sign test

and first observation, showed a clear restriction to the lower reaches, I conclude that emergence took place (almost) exclusively in the lower reaches of the stream. The newly emerged individuals stayed in the area of the lower reaches as long as their wings showed an immature coloration. Shortly after attaining mature coloration, however, a substantial proportion of the population must have shown a net upstream movement in order for the distribution pattern of the mature individuals to be achieved. Observations of immature individuals were few as compared to those of mature ones. This difference may be for several reasons – intensive search being limited to short distances from the water; the lateness of the periods of observation in most years; cryptic behaviour of teneral (Heymer 1973) – the result of which was that I could have missed a large proportion of the immature individuals.

As far as I am aware, there are no other published records on differential distribution of zygoptera along streams. Corbet (1999: 646) mentions only a few examples of Anisoptera species, belonging to the genera *Cordulegaster* and *Epiophlebia*, which showed a greater abundance of young larvae in the upper reaches of a stream. Direct evidence in favour of larval drift appears to be scarce in Odonata (Corbet 1999: 15, 394). As judged from the regular presence of fresh debris well above the summer water levels, in the studied stream, periods with strong currents must have occurred in all years and in such periods substantial larval drift may have occurred. Thus larval drift will be a likely explanation for the differential distribution of on the one hand mature individuals and reproductive activities taking place along the entire stream (compare distribution of territories shown in Fig. 1) and of on the other hand immature individuals, including teneral, indicating the location of emergence sites. These observations on the distribution of immature individuals do not exclude the possibility that some of them originated from even lower sections of the valley (downstream of the regularly surveyed sections), particularly during the week before I started my observations. This does not change the line of reasoning, but any downstream movement of immature individuals would do so. As the distribution patterns of teneral and older immature individuals matched, such movement should have taken place during the day of emergence and during the hours before my first daily survey. The capacity of teneral to fly is so low in the first half of the day of emergence that I consider such downstream moves over hundreds of m to be unthinkable.

Evidence for upstream movements immediately after the attainment of mature wing coloration is shown in all three columns of Table 2. The group of ‘maturing’ males (and probably also that of similarly aged females) showed some special characteristics in frequency, direction and distance of movements, viz a high day-to-day mobility, long net displacements, and an upstream bias in these moves. These traits were rarely present in other adult life stages. Thus the upstream movements took place during the first week after the wing coloration had become indistinguishable (at some distance) from that of mature individuals when a fully mature stage had not yet been reached, as judged from incomplete abdominal-spot coloration and absence of reproductive behaviour. The upstream bias in movements of maturing individuals would explain the difference in distribution patterns along the stream of mature and immature *C. haemorrhoidalis* and thus of the locations where reproduction and emergence prevail, i.e. this upstream bias could compensate for larval drift. Published observations on displacements in

adult calopterygids (Table 3) point to prevalence for upstream-biased movements in the immature stage (see examples in *C. splendens* Harris, *C. cornelia* (Selys) and *C. haemorrhoidalis*). Such upstream movements are also known in some Anisoptera, viz in species of *Octogomphus*, *Stylogomphus* and *Zygonyx* (Corbet 1999: 646). Thus, larval-drift compensation by upstream-biased adult movements may be widespread in Odonata.

Table 3. A summary of published observations on upstream or downstream movements of adult calopterygids (*C.* = *Calopteryx*, *H.* = *Hetaerina*); > = more, >> = many more.

Species	Direction	Life stage	Sex	Reference
<i>C. atrata</i>	up (occasionally)	-	both	Miyakawa (1982)
<i>C. cornelia</i>	up >> down	immature	-	Higashi & Ueda (1982)
<i>C. haemorrhoidalis</i>	up > down	immature	male	Cordero (1989)
	up = down	mature	male	
<i>C. haemorrhoidalis</i>	up >> down	maturing	male	present paper
	up > down	mature	male	
<i>C. splendens</i>	up >> down	immature	both	Groot & Smit (1954)
<i>C. splendens</i>	up > down (long distances only)	-	-	Schutte et al. (1997)
<i>H. cruentata</i>	no preference	all	-	Cordoba-Aguilar (1994)

The observed net upstream displacements do not necessarily point to unidirectional migrations by maturing males. It might well be that these net displacements resulted from random probing of attractive sites to establish a territory. Suitable vacant sites will always have been available, as the number of occupied sites never exceeded about ten per 80 m of stream length and territorial males that were displaced by the experimenter frequently succeeded in establishing a territory at a new location (Beukema 2002). However, the most attractive sites will mainly have been occupied. This will have been true in all three high-density years, because the distribution of territories over the sections of the stream was similar in these years. Maturing males, searching for a territory site, will have been chased away from the most attractive sites by older established males. I saw maturing males generally at greater distances from the water and could chase them away more easily than established males, which had already been defending a site for several days. Thus, maturing males will often find a territory only after having been chased away at other places. This means that they have to move over some distance before they can establish themselves somewhere. For an individual starting its movements in the lower reaches and flying for relatively long distances, as maturing individuals do, the result will more probably be a net movement upstream rather than downstream, because the lower end of the stream, where the habitat became unsuitable, will be reached more rapidly. In conclusion: any special ability for executing

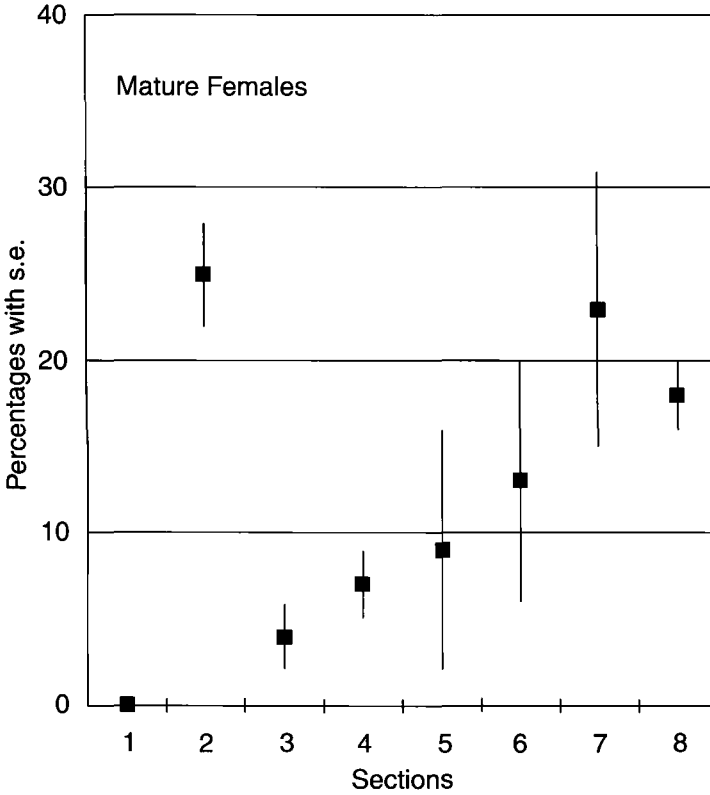


Figure 2. *Calopteryx haemorrhoidalis* — relationship between an index of density of territories, expressed as mean number of territories observed per 80 m section of the stream in a certain year, and its coefficient of variation ( $n = 8$ , i.e. number of sections). One point for each of the five years of observation. A lower coefficient of variation means a more even distribution of the territories along the stream.

directed movements, e.g. guided by current direction, is not a prerequisite for the observed upstream-biased net movements.

The more even distribution of territories along the stream at high than at low numbers of territories (Fig. 2), also points to the establishment of territories at places that were still vacant and not solely at the first suitable site encountered by a maturing male. In this way the final distribution pattern of territories along a stream, is reached by a density-dependent process. Such a process might also contribute to upstream movements. If the first maturing males of the reproductive season establish their territories along the lower reaches close to their emergence sites, the later-maturing males will be forced more and more to upper reaches. Because the distribution pattern of territories along the stream had already taken its final shape by the first half of June, possible higher initial territory densities along lower rather than along upper reaches might be an important force in net upstream movements for only short periods at the

very beginning of the reproductive season, i.e. in the second half of May only, as the first adults emerge in late April or early May. During the majority of the reproductive season, however, all sections of the stream will have offered similar opportunities to newcomers. Then, the observed bias in the direction of the moves appears to result merely from the combination of the initial bias in the distribution of the immature individuals (i.e. along the lower reaches only) with roughly equal chances of establishment of a territory at all parts of the stream (including the upper reaches). The only requirements are then an ability to fly distances in the order of some hundreds of m and an inclination to leave a site after a lost territorial dispute. Both requirements are easily achievable and in accordance with observations. An innate tendency of adults to fly upstream appears not to be necessary to explain the present results. As also argued by Anholt (1995), the existence of a density-dependent process – in the present case: high-density driven movements resulting from territorial fights – is sufficient to explain the regular repopulating of the depleted upper reaches of the stream. The close correspondence of the average distance between the territories and the source of the stream in different years, with between-year differences of <5% of the stream length, points to an exact compensation of stream drift, which appears to be the most favourable strategy, according to model studies by Kopp et al. (2001).

### Acknowledgements

I am grateful to the owners of the camping site Can Banal for their hospitality and for allowing me free access to their grounds. Marcel Wasscher brought the *Calopteryx* population of the Can Banal area to my attention.

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