

**SURVIVAL RATES, SITE FIDELITY AND  
HOMING ABILITY IN TERRITORIAL *CALOPTERYX*  
*HAEMORRHODALIS* (VANDER LINDEN)  
(ZYGOPTERA: CALOPTERYGIDAE)**

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In a small isolated population along a small stream in NE Spain, a high proportion of the adults present were individually marked. During subsequent days, their locations were assessed by twice-daily surveys along the entire length of the stream. Mean daily survival rates in mature ♂♂ and ♀♀ and pre-reproductive ♂♂ were similar, 94%. Only during the first day after marking were survival rates significantly lower (viz. 77 to 84% in the various groups). High proportions (around 90%) of mature ♂♂ were found to return to the same (territory) site every morning once they had occupied that site for 2 or more days. Site fidelity was low in pre-reproductive ♂♂ and intermediate in mature ♀♀. In a displacement experiment, 67 territorial ♂♂ were transferred one by one to distant locations (80 to 240 m along the stream). Half of them returned to their original territory, usually on the same day.

**INTRODUCTION**

In many species of Odonata, including the Calopterygidae, mature males defend a territory against conspecific males and guard conspecific females ovipositing within it. In some species, territorial males have been observed to use the same location day after day as a territory, thus showing strong and persistent site fidelity. CORBET (1999) lists 28 species in which males have been observed for periods of 10 or more days at the same territory site. This list includes *C. virgo* with a maximum of 40 days (KLOTZLI, 1971), *C. haemorrhoidalis* with 19 days (HEYMER, 1973), and *C. splendens* with 13 days (ZAHNER, 1960), including interruptions for short periods, e.g. due to adverse weather conditions. These records clearly show the existence of long-term attachment to specific territory sites. However, they usually lack further information, such as frequency of shifts to other sites and dependence on age. In the

non-territorial females and immature males, lower site fidelity is expected, but any attempt to quantify the expected difference with reproductive males appears to be lacking. Moreover, data on site fidelity should be incorporated into a study of population dynamics, because the chance of encountering an individual on subsequent days at the same location is affected by its daily survival rate and estimates of duration of site fidelity should be compared to those of longevity. Therefore, estimates on survival are indispensable in a study on site fidelity.

If males leave their territory in the evening to spend the night away from the water (as e.g. *C. haemorrhoidalis* males do), multi-day site fidelity should involve an ability to return to the right spot and recognize it; i.e. territorial males should be able to use some memory of the characteristics of their territory and of its surroundings to efficiently return to it on subsequent days.

In the present paper, I describe results of marking experiments in a small population of *Calopteryx haemorrhoidalis* (Vander Linden) living along a small stream in northeastern Spain. Several hundred adult males were marked individually. By daily surveys of the entire area occupied by the population, the presence along the stream and the exact location of marked individuals was assessed during subsequent days. Because high proportions of the marked individuals were frequently resighted, these observations allowed not only an estimate of total local daily survival rates (the proportion of animals that did not die nor disperse from the stream section surveyed), but also of chances to resight them at the same site. By displacing territorial males and frequently watching their territory and adjacent areas, the probability and speed of their return were estimated.

## METHODS

The populations 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 Girona province. The stream is called Torrente del Estanyol and its location is indicated on a map by 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. As this rocky valley lacks almost any vegetation and dries up in the course of most summers, it is unsuitable for *Calopteryx* territories. Therefore, the studied adult population appears to be isolated from suitable neighbouring habitats, since these were more than 1 km away and separated by dry woodland and rocks.

In summer, the width of the stream locally varies between 0.3 and 5.0 m, its depth between 0.1 and 1.0 m, but after heavy rain the water level may be up to 1 m higher as judged from debris washed up in the shrubs. The bottom is chalky with numerous ridges, slowing down the current speed and creating numerous pools. The borders are mostly wooded with tall trees and shrubs along most of the 650-m stretch, but sunny spots are numerous on and along the water. However, most of the total water surface is in the shade more than half of the day, leaving only limited suitable areas for territories. Water temperatures 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 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) *Calopteryx* appeared near the water on such days.

The populations were surveyed during 12 to 20 successive days (interrupted only by a few days with inclement weather) in each of 7 years, as listed in Table I. Highest numbers of *Calopteryx* were present between 11 a.m. and 5 p.m. (as also observed along the same stream by WASSCHER, 1996). On days with suitable weather, all potential territory sites were inspected at least twice per day. The survey track followed the stream, nearly entirely by wading. As many as possible males (and also several females) were caught by gentle netting and marked by a unique combination of white and/or red paint 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. Numbers of marked individuals ranged from 14 to 176 in the 7 years, totaling 559 (Tab. I). Marking place, sex and a rough estimate of age were noted. An individual was noted as immature if it did not yet show the full mature wing coloration. After about one minute (to allow the paint to dry), a marked individual was released at the same place, where it usually flew up into the trees. 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 m.

To investigate their homing ability, 67 marked males were caught within their territory, moved in a closed net to a location at the stream between 80 and 240 m away, and released within about 10 min after catching. These males had been marked several days before and resighted at the same site for at least 4 days to assess that they were owners of a fixed territory. During subsequent surveys (the first one usually on the transfer day), their position along the stream was recorded as frequently as feasible (usually twice daily).

The  $\chi^2$  test was used throughout the paper to evaluate statistical significance of observed differences in numbers.

## DAILY SURVIVAL

In all years, most of the marked individuals were seen again during subsequent surveys. The resighting percentages were generally slightly higher in males than in females, but the difference was not significant ( $0.05 < p < 0.1$ ), whereas the difference between mature and immature individuals was far from significant (Tab. I).

Table I

Numbers of prereproductive (immature) and mature males and females of *Calopteryx haemorrhoidalis* marked and percentages (%) seen again on at least one subsequent day in each of seven observation periods. — [After a few days of marking effort, the numbers of marked individuals included nearly all truly territorial males and most of the other mature males, but only low proportions of the females and immature individuals]

Year	Period	Number marked				Percentage resighted			
		males		females		males		females	
		imm.	mature	imm.	mature	imm.	mature	imm.	mature
1991	12/VII-23/VII	0	36	0	0	81			
1992	13/VII-27/VII	0	32	0	4	75		25	
1993	14/VII-02/VIII	4	142	0	30	50	85		83
1994	28/VI-15/VII	1	9	0	8	100	100		100
1996	19/VI-07/VII	3	102	0	27	100	89		78
1997	06/VI-25/VI	26	83	10	28	77	83	70	79
1998	12/VI-22/VI	1	7	0	6	100	71		50
Totals		35	411	10	103	77	84	70	78

The daily records of the marked individuals were used to assess minimal numbers and percentages of individuals still alive on successive days after marking for use in calculations of daily survival rates and mean longevity. Effects of overlooking by the observer during surveys or absence of the damselfly along the survey track due to adverse weather conditions could partly be nullified by considering individuals encountered on a certain day to have been alive on all foregoing days between the marking day and the day of observation. Nevertheless, it should be kept in mind that the survival estimates are bound to be underestimates, because the observer will certainly have overlooked some individuals before the day of their death.

The percentages of marked individuals still alive gradually declined at a regular rate during the first ten days after marking when numbers were still high and estimates were relatively precise (Fig. 1a). The best fitting lines through the points shown in this Figure run slightly curvilinear, becoming linear on a logarithmic plot starting from day-1. This points to a constant daily rate of survival starting from 1 day after marking. These lines run almost parallel in males and females, corresponding to a daily survival rate of 94% between days-1 and -10 in both sexes (Fig. 1a). Neither did the survival rates of immature and mature males differ (Fig. 1b). Low numbers of marked immature females did not permit a separate survival estimate for this group.

The above estimate of daily survival of 94% did not apply to the first day after marking (day-0 to day-1). On this initial day, survival was substantially lower than 94% in all groups, viz. 84% in mature males, 78% in mature females and 77% in immature males. Differences between survival rates for the first and the second day

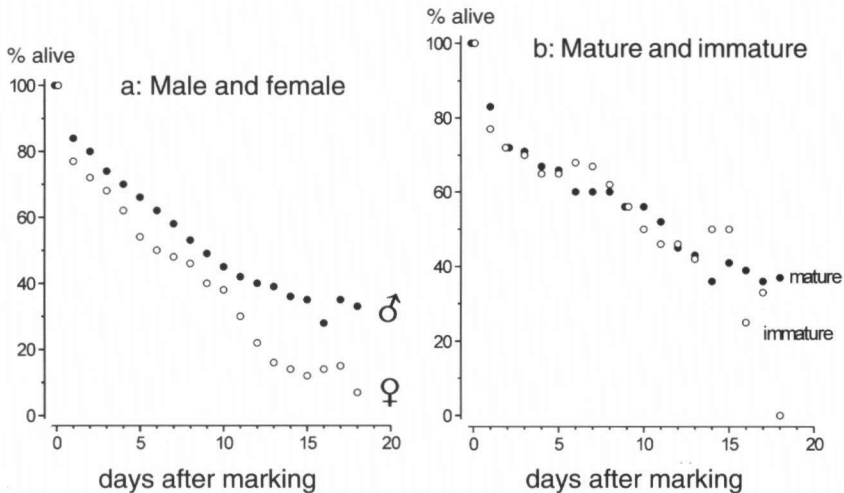


Fig. 1. *Calopteryx haemorrhoidalis*, minimal percentages of groups of marked damselflies still alive on successive days after the marking at day-0: (a) summed observations (added data of all 7 periods of observation) on 446 marked males (●) and 113 females (○); — (b) observations made in 1997 on 83 individuals marked as mature (●) and 26 as immature (○) males.

after marking were statistically significant both in males ( $p < 0.01$ ,  $n = 446$  and  $373$ ) and in females ( $p < 0.01$ ,  $n = 113$  and  $87$ ). Apparently, there were extra losses of between  $\sim 10\%$  and  $17\%$  immediately after marking. In other words, handling for marking roughly tripled the normal daily disappearance rate of  $6\%$ . The present methods do not allow making a distinction between mortality, emigration, and additional mortality brought about by being handled.

### SITE FIDELITY

During the evening, night and early morning, *C. haemorrhoidalis* were not present along the survey track. They were probably roosting at communal roosts high above the water surface, invisible in the crowns of the trees. They were seen to descend in the course of the morning, but number and location of the roosts could not be assessed. Reproductive males took a territory generally between 10 a.m. and noon. Marked individuals were usually resighted at the same site (often even on the same perch) where they had been seen on the previous day. Along the regularly surveyed stretch of the stream, about 60 sites were suitable for a territory (i.e. these places were found to be frequently occupied by a territorial male). I defined and named such suitable sites with a diameter of generally several meters. These sites were larger than the small areas (a few  $\text{m}^2$ , compare also the even smaller  $0.5$  to  $1.5 \text{ m}^2$  given by CORDOBA-AGUILAR, 2000) actually defended at any time. This was a consequence of the males' tendency to change his perch within these sites according to the sunlit parts, which could shift several m in the course of the day. Therefore, it was inevitable to record an individual as being at the same site if it was present within about  $5 \text{ m}$  from the location of the preceding observation.

To quantify site fidelity, I expressed it as a percentage of all resights of an individual that were at the same site (within  $5$

Table II

Site fidelity (%) in mature females and in various adult life stages of males of *Calopteryx haemorrhoidalis*. — [N = number of observations. Statistically significant differences between two figures are indicated by symbols placed in between the compared figures only as far as the comparison is considered to be meaningful: ° = non-significant, \* =  $p < 0.05$ , \*\* =  $p < 0.01$ , and \*\*\* =  $p < 0.001$ ]

Sex and condition	Data of:	
	1997 only % (N)	all other years % (N)
Females:		
all mature	53 (112) **	60 (182) ***
Males:		
all mature	69 (296) ***	78 (1682)
imm. coloured	40 (40) °	***
rec. mature	47 (32) ***	***
territorial >4d	92 (127) *	95 (339) ***
last days territ.	77 (13)	60 (15)

m) as the last observation of that individual. The last observation was usually on the previous day, but may have been more than one day earlier, e.g. if weather was bad on the intervening day. Table II shows a summary of the observed resight percentages, separately for 1997-only and for all other years together (1997 was the only year with a high number of immature individuals at marking, allowing separate estimates for groups of males of different known age and maturity state).

As expected, mature females showed significantly lower site fidelity than mature males (Tab. II: top rows). Among the males, site fidelity was dependent on their life stage. Those with clearly immature colours and individuals that had only recently (< 3 days before) attained mature coloration ("rec. mature" in Tab. II) showed

significantly lower site fidelity than fully mature males. Site fidelity was particularly high (well above 90%) in mature males that occupied a certain territory already for several (> 4) days. However, it declined during the last two days of their life, viz. to a significantly lower percentage of 60-77% in males that had occupied a territory for > 4 days during the period immediately preceding the last two days they were resighted (Tab. II). It will be meaningful that the few observations of a territorial male losing a territorial fight, were just before the end of the resighting period in that male.

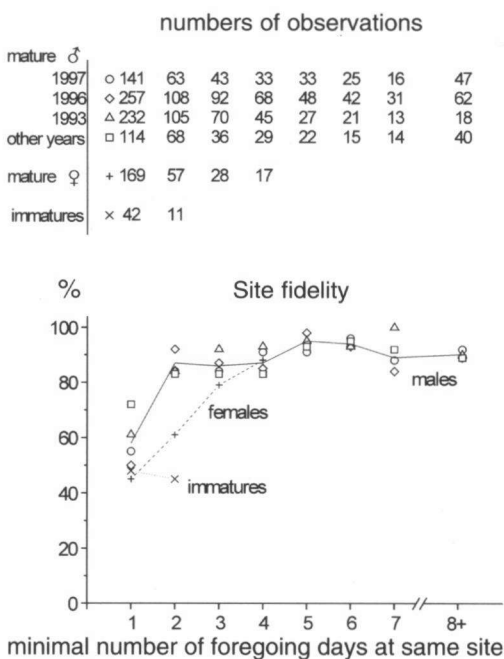


Fig. 2. *Calopteryx haemorrhoidalis*, percentages of individuals that were resighted at the same site (i.e. within ~ 5 m of the former site) after having been seen there on 1, 2, 3...8 or more preceding days (without interruptions of sightings at other sites). Data on three groups presented separately: mature ♂ (○ = 1997, ◇ = 1996, △ = 1993, □ = summed data of 1991, 1992, 1994, and 1998; totals of all 7 years indicated by an uninterrupted line); — mature ♀ (+ and dashed line; totals of all years); and — immature individuals (× and dotted line; totals of all years). A percentage is shown only if >10 observations were available (see number of observations given at the top of the Figure).

Site fidelity percentages were positively related to the number of days an individual had already been present at a certain site. If I had seen a reproductive male at a certain site on two or more days (without intervening days at another site), the chance that the next resighting would be at the same site (and not elsewhere) was ca 90% and even higher (ca 95%) if the individual had kept the same territory for more days (Fig. 2:

open circles). These high site fidelity percentages after two or more days at the same site were significantly ( $p < 0.001$ ) higher than the percentages of ca 60% found after a preceding stay at that site of only one day. Note that such one-day-only observations constituted a heterogeneous group, since this group included not only individuals that had really stayed there for only one day but also individuals that could have been present there also on earlier days but were not yet marked or observed. This means that site fidelity must have been lower than ca 60% in mature males that had been at a certain location for only exactly one day. Site fidelity in recently matured males (those not yet truly territorial) amounted to 47% (Tab. II). As a consequence of the relatively low site fidelity in young (though looking fully mature-coloured) males, male site fidelity tended to increase in the course of the season (June-August), reflecting the increase of the proportion of fully reproductive males.

In immature males, the percentages occurring at the same location as on previous days were not only lower than in mature males. Another difference was that these percentages did not show an increase with numbers of days they had been seen at this site (Fig. 2: the x points). Though immature individuals did not show a clear attachment to a site, almost half of the resightings on later days were at roughly the same location, i.e. within about 5 m, but not at specific perches and generally several m away from the water surface (as opposed to fully reproductive males, who were often observed at the same perch close to the water surface day after day). Generally, the reproductive males were resighted every day (weather permitting), whereas often several days elapsed between successive resightings of immature individuals.

In mature females, site fidelity percentages were mostly low (ca 50%), but increased to levels similar to those of reproductive males once an individual female had been at the same site for three or more days (see Fig. 2, + points and dashed line; the differences were significant between 1 and either 2, 3, or 4 days, and between 2 and 4 days). The differences in site fidelity between mature males and females (uninterrupted and dashed line in Fig. 2, respectively) were significant ( $p < 0.01$ ) after 1 and 2 days, but not after 3 or 4 days. The high site fidelity values in mature females after stays of 3 or more days at the same site were due to a low number of individuals that returned to the same site day after day. Most females were resighted less frequently and mostly at sites that differed from day to day (observations of these females are included in the relatively large 1-day group in Fig. 2, cf. numbers of observations).

A high site fidelity of about 90%, as observed in territorial males, means that individuals usually stick to the same site for several days in succession. Long series of 10 or more days were not at all rare (though such series were frequently interrupted by one or two days if weather was bad). Such long series were observed in about 50 males.

The longest period a territorial male was seen at the same location was 20 days, but this will be an underestimate, since the longest survey period lasted only 20 days (in 1997, see Tab. I).

Table III

Numbers of territorial males of *Calopteryx haemorrhoidalis* transferred to another site at the stream, and either never seen alive on subsequent days, or resighted at their original territory site, at the release site, or elsewhere (either between the release and the territory site or beyond this stretch of the stream)

Year	Transferred number	Never resighted	Location of first resight after transfer			
			Territory site	Release area	Between	Beyond
1992	11	2	6	3	0	0
1993	35	6	15	6	5	3
1996	21	2	9	4	4	2
<i>Totals</i>	<i>67</i>	<i>10</i>	<i>30</i>	<i>13</i>	<i>9</i>	<i>5</i>

### HOMING ABILITY

By far most (57) of the 67 transferred males were resighted at subsequent surveys along the stream. The loss of 10 individuals appears to be somewhat in excess of the normal daily mortality of 6%, but the extra handling (catching and moving) may have enhanced the disappearance rate as observed immediately after initial marking (see above).

About half (30) of the 57 survivors among the transferred males were encountered afterwards at the site of their original territory (Tab. III). Quick returns, already completed on the day of the transfer, were observed in 19 males. The proportion of quick returns was certainly underestimated, since some of the moves would have taken place after the last survey of the day.

Nearly half of the 27 individuals that did not return to their territory were observed to stay at the release site. Many of the others were resighted somewhere between the release and the original territory site, but 5 males had moved into the "wrong" direction (Tab. III). Many more males had moved into the "right" than the "wrong" direction, viz.  $30 + 9 = 39$  versus 5. Thus, a hypothesis that their return flight resulted in a net movement into a random direction can be rejected ( $p < 0.001$ , sign test with  $n = 44$ ).

Results of upstream transfers did not differ from downstream moves: returns to the original territory were 16 out of 36 upstream moves and 14 out of 31 downstream moves.

The distance of the moves may have affected the return success. After short moves (80-140 m), 24 out of the 49 transfers resulted in a successful return, whereas this was so in only 6 out of the 18 longer moves (160-240 m). The difference, however, was far from significant ( $p > 0.1$ ). It should be noted (1) that even the shortest distances of about 80 m did never allow a direct view to the territory site (direct views along the stream were usually limited to  $< 10$  m as a consequence of dense vegetation of shrubs in nearly the entire valley) and (2) that several other territory sites were located between the sites of the release and the original territory.



## DISCUSSION

## SURVIVAL

Calopterygid damselflies are well suited for population studies by individual marking since they are easily caught and resighted. The present population of *Calopteryx haemorrhoidalis* was sufficiently small (numbering at most a few hundred) and lived in a sufficiently confined area to be efficiently surveyed, allowing high proportions of all individuals to be marked and high chances to resight marked individuals. Because of its isolated habitat, emigration rates will have been low. The observed high value (94%) of mean daily survival rate excludes any high rate of emigration.

The mean survival rate observed in the present study (0.94 per day) was similar to rates observed in other calopterygid species, ranging from 0.70 to 0.98 per day (Tab. IV). Extremely low and high values observed by some authors deserve closer inspection. The low (0.70 and 0.77) figures in *C. aequabilis*, reported by CONRAD & HERMAN (1990) were found in a population with a high proportion of migrants and therefore may reflect a high daily rate of emigration rather than mortality. The exceptionally high figure of 0.98 in *Hetaerina cruentata* reported by CORDOBA-AGUILAR (1994) was derived (in an unexplained way) from greatly fluctuating individual values (including nonsense values of > 1). A recalculation, using data shown in figure 3 of

Table IV  
Published estimates of mean daily survival rates in *Calopteryx*, *Hetaerina* and *Mnais* species

Species	Country	Survival (per day)	Sex	Reference
<i>C. aequabilis</i>	Canada	0.77 0.70	♂ ♀	CONRAD & HERMAN (1990)
<i>C. atrata</i>	Japan	0.91* 0.93*	♂ ♀	MIYAKAWA (1982)
<i>C. haemorrhoidalis</i>	Spain	0.94 0.94	♂ ♀	present study
<i>C. japonica</i>	Japan	0.82/0.87 0.93/0.87	♂ ♀	WATANABE et al. (1998)
<i>C. virgo japonica</i>	Japan	0.94* 0.97*	♂ ♀	MIYAKAWA (1982)
<i>H. cruentata</i>	Mexico	(0.98)/0.94**	♂	CORDOBA-AGUILAR (1994)
<i>M. pruinosa</i>	Japan	0.94	♂	HIGASHI (1976)
<i>M. pruinosa</i>	Japan	0.955	♀	NOMAKUCHI et al. (1988)
<i>esakii</i>		0.944	♂	
<i>strigata</i>		0.947	♂	

\* As calculated from histograms of survival rates shown in MIYAKAWA (1982), including only survival between 1 to 10 days after marking.

\*\* Recalculated value, see text.

CORDOBA-AGUILAR (1994), yielded an estimate of 0.94, and this figure is more in line with records for mean daily survival in Calopterygidae by other authors. Exclusion of the above questioned extreme values narrows the range of published values to 0.82–0.97, with a preponderance of survival rates close to 0.94 per day (Tab. IV). This may, therefore, be a typical value for calopterygid species.

Survival during the first day after marking appears to be generally lower than mean survival, as can be deduced from detailed data given by HIGASHI (1976), NOMAKUCHI et al. (1988) and own observations (Fig. 1). It is questionable whether the enhanced disappearance rates immediately after marking point to higher death rates (by rough handling) or to handling-induced changes in behaviour (stronger tendency to migrate).

The above figures for mean daily survival in Calopterygidae are mostly higher than the values generally recorded in Zygoptera, ranging from 0.73 to 0.94 (CORBET, 1999: 301). The relatively high values found in Calopterygidae may partly be caused by their site fidelity, conspicuousness, and tameness. This is especially true for reproductive males and may (partly) explain the different levels for males and females in percentages found alive as shown in Figure 1a. Probably, there was no real difference in daily survival rates between males and females in the studied population, since the data sets of the two sexes shown in Figure 1a run parallel. Differences between males and females were also small in other species (Tab. IV) and were not consistently higher in either sex.

The effect on estimates of survival rates of overlooking a certain proportion of the marked individuals can be judged to some extent by omitting all observations on individuals that were marked shortly before the end of the observation period in each year. If the calculations are limited to individuals that could potentially be resighted for > 7 days, the percentages resighted slightly rose from 84 to 86 in mature males and from 78 to 82 in mature females. Note that the extension of the observation period to >7 days appears to have enhanced the chance to re-encounter a female more than that of a male, as expected from differences in their conspicuousness (particularly during oviposition females may easily be overlooked). Though all estimates of survival rates from resightings are bound to be underestimates, the bias appears to have been small in the present study.

A mean daily survival rate of 0.94, as observed in the present study for the two sexes and age groups, would mean that the size of the adult population halves in about 11 days. This is roughly the duration of the maturation period in *C. haemorrhoidalis* (HEYMER, 1973; CORDERO, 1989; own observations). Maximum longevity cannot be stated exactly, because the number of very old individuals that can be observed depends among other things on the population size and the searching effort of the observer (BEUKEMA, 1989). At the above survival rate, about 1% of all emerged individuals will live at least 74 days as an adult. In a population of the present size, the maximum adult life span would thus amount to two or three months (if there were no increased mortality at high age by senescence). In the field, the oldest individuals

HEYMER (1973) recorded in *C. haemorrhoidalis* must have lived at least 37 and 39 days as an adult. CORDERO (1989) recorded a maximum age of 43 days in this species. TSUBAKI et al. (1997) found maximum ages in the field of 55-60 days in males of the two colour forms of *Mnais pruinosa*. As noted above, these field records are bound to be underestimates of maximum longevity. A high age of >80 days was actually recorded for captive *C. splendens* (LINDEBOOM, 1993, cited from CORBET, 1999: 302).

#### SITE FIDELITY

A high degree of site fidelity, as evidenced from a high incidence of multi-day resightings at the same locations of marked individuals, is not uncommon in territorial males of Calopterygidae (*C. haemorrhoidalis*: HEYMER, 1973; CORDOBA-AGUILAR, 2000; and present study; *C. splendens*: ZAHNER, 1960; *C. virgo*: KLÖTZLI, 1971). In the present study, it was also observed in a small number of mature females (cf. Fig. 2: dashed line) and this is an unexpected result.

Site fidelity was low in immature males (Fig. 2; Tab. II) and increased only significantly some days after males had attained mature coloration. At that stage, males stayed longer and longer at the same location at the stream and chose perches close to the water surface. Initially, they could be chased away easily and then flew far away (often to the canopies of the trees). After they had stayed more days at the same site, they could less easily be disturbed and returned more rapidly to their preferred perch. In this way, a strong site fidelity of > 90% developed (solid line in Fig. 2). Such high site fidelity values were also observed in a few females, but the increase with number of fixed-site days was less steep than in males and only a low proportion of the females attained this high site fidelity (as opposed to probably all of the maturing males).

Maximal values of site fidelity of over 90% were recorded in males that had successfully defended their territory already for several days (Fig. 2, Tab. II). The chance that they would be encountered the next day at the same site was similar to their daily survival rate of 94%. This means that virtually all of the territorial males that stayed alive will have returned to the territory site of the previous day. Only during the last few days of their life do they appear to run a higher risk to lose it (bottom line of Tab. II). In the population of *C. virgo* studied by KLÖTZLI (1971), changes of territory site occurred particularly frequently during the first and last few days of their territorial lifetime. Thus, as in the present study, both recently matured and almost senescent males more often moved to another site than males in the middle of their reproductive period. Probably, they had to do so as a consequence of losing fights with other males. During the very height of their territorial period in the present study, the males showed a rate of site fidelity nearly equaling their survival rate; i.e. site fidelity was almost complete in surviving males.

The detailed data given by KLÖTZLI (1971) allow a precise comparison (after some calculus) with the data shown in Figure 2 for mature males. Over the entire range

of occupation times, site fidelity was higher in the present population of *C. haemorrhoidalis* than in the studied *C. virgo* one. This was particularly so after short occupancies (1 day: 58 vs 46%; 2 days: 87 vs 67; 3 days: 86 vs 77; 4 days: 87 vs 76; 5 days: 95 vs 77; 6 and more days: 89-94 vs 88-91%). Nevertheless, KLÖTZLI (1971) recorded a maximum stay of no less than 40 days at the same location (though there was a fortnight-interruption without observation data).

Most females showed a site fidelity percentage of around 50%, hardly higher than in immature males (the number of observations in immature females was low and their site fidelity was similar to that of immature males). Even a percentage of 50 means that the individuals had a rather strong tendency to return every day to the same location (within about 5 m). Probably, they descended every day along the same route from their roosts to the same sunny spots along the stream.

#### HOMING ABILITY

Territorial males of *C. haemorrhoidalis* have to cover some distance every morning to return to their territory site after having spent the night at distant communal roosts. These distances appear to amount to some tens of m (HEYMER, 1973: 20 to 100 m; NEUBAUER & REHFELDT, 1995: a range of 6 to 48 m with a median value of 34 m). In the present population, I could not estimate this distance; in the late afternoon the damselflies disappeared somewhere high in the canopies of tall trees at distances of >10 m from the water, where I could no longer follow them. Due to the presence of tall trees along the stream, all locations near the water were shaded during the first hours after sunrise and the last hours before sunset; for roosting sites damselflies prefer exposure to the sun during such hours (NEUBAUER & REHFELDT, 1995). Covering such long distances to reach the territory site in the morning certainly requires some ability to navigate and to recognize the site. However, it is doubtful whether all possible abilities (e.g. a sun compass) discussed by CORBET (1999: 388) would be necessary because mere recognition of landmarks could be sufficient. Any details on how exactly these damselflies manage to home appear to be unknown. The homing phenomenon, however, clearly exists and is borne out by results of my displacement experiments.

HEYMER (1973) displaced 50 mature (but non-territorial) males of *C. haemorrhoidalis* in the morning to a point 2 km away from the capture area at the same stream. Following the watercourse, slightly more than half of the displaced individuals returned to the 300-m stretch of the stream where they had been captured earlier that day. It is not clear from HEYMER (1973) whether the other half of the individuals followed the stream into the "wrong" direction or took the "right" direction but stayed somewhere in between the release and capture area. Nor does this experiment tell us whether the animals recognized specific parts of the 300-m stretch to stay there.

In the experiments described in the present paper, again about half of the displaced (exclusively territorial) males succeeded to return. In this case they returned exactly to their territory site, where they remained that day and mostly for several subsequent

days, continuing the defense of their original territory. The few individuals that I could observe during a part of these flights followed the stream, flying rapidly for long distances at  $< 1$  m above the water surface in an almost straight line, keeping roughly the middle of the stream. I saw this "purposeful" type of flying only occasionally in other males. Such males covered long distances in this way and were far away from places where they were seen more often. During such flights, individuals may learn characteristic landmarks to be used whenever they are away from their territory site.

Two hypotheses can possibly explain the high proportion of the transferred males that returned exactly to their original territory (Tab. III), viz. (1) they recognized their earlier territory site, or (2) this site was (almost) the only one available along the stream (and there is no need for an ability to recognise specific sites). The latter hypothesis would be probable only if nearly all other suitable sites along the stream were occupied by the maximum number of males. This was certainly not the case, as 13 transferred males succeeded to remain at the release site (Tab. III), often for several days and mostly successfully establishing a territory. This occurred also in the 14 males that stayed at other places. At the usual density of a few to about 10 territorial males per 100 m of stream bank, there were plenty of empty suitable sites at every 100-m stretch and some of these were immediately used by the males that did not return to their original territory site. Thus, it is improbable that released males were chased away everywhere until they finally happened to arrive at their former (possibly still vacant) territory site. Of course, on their way to their original territory site they will have passed occupied territories where they were chased away, but they also will have encountered several unoccupied potential territory sites. This was particularly so in the year with low adult densities (1992, see Tab. I), but the various proportions shown in Table III did not differ significantly from those observed in the higher-density years 1993 and 1996. Random choices of unoccupied sites by returning males (into the right direction) would have resulted in some 10 or 20% matches with the original territory sites (or even less if they would choose the first free site to occupy), amounting to some 5 or 10 matches and this number is significantly lower than the realized number of 30 (Tab. III). Therefore, the results of the transfer experiment can be considered as genuine evidence for an ability of site recognition by territorial males.

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