Space use in territorial and non-territorial male *Calopteryx splendens* (Odonata: Calopterygidae)

Alexey S. Opaev & Evgeniy N. Panov

A.N. Severtsov Institute of Ecology and Evolution of the
Russian Academy of Sciences, Moscow 119071, Russia;
<aleksei.opaev@gmail.com>

Abstract. In *Calopteryx* damselflies male territorial and non-territorial alternative mating tactics are identified. Territorial males are believed to secure more copulation. With increasing age, males starve and become non-territorial that only occasionally manage to copulate. However, space use of territorial and non-territorial males is not known in detail. We present the data on space use of individually marked male *Calopteryx splendens* (Harris, 1780), obtained during two field seasons in Vladimir Oblast, Russia. Each damselfly was captured, marked and the wing length was measured. During observation sessions of 2–4 hours per day, each male was characterised as either territorial or non-territorial and encounter locations were mapped. The probability of being territorial declines with the male's age. Territorial *vs* non-territorial tactic in a given day strongly influences tactic retention on the next day. We identified the territorial and non-territorial phases in the life of a male, which occur consequently and have roughly similar duration. We define the territorial phase as all days until the last record of a male as a territorial individual. The subsequent days were defined as the non-territorial phase. During the territorial stage, males may (1) occupy a single territory; (2) be non-territorial in some of the days and then return to his previous territory or (3) after staying within a certain territory for several days change it and occupy another territory on the next day or several days later. The transition from the territorial to the non-territorial phase is gradual. It may suggest this transition caused by exhaustion. Thus, space use changes predictably during the life of a male. Characteristics of individual lifetime trajectory – number of days when the male was recorded as territorial, number of territories occupied, etc. – did not depend on wing length.

Further key words. Dragonfly, damselfly, Zygoptera, behaviour, Russia.

Introduction

In a number of damselfly species males are known to show intraspecific variability of space use and reproductive behaviour (Poethke 1988; Rehfeldt 1991; Suhonen et al. 2008). Males use two or three alternative mating tac-

tics (Fincke 1985; Banks & Thompson 1985; Forsyth & Montgomerie 1987). Differences between the tactics often, but not always, involve different use of space. Territorial males defend small vegetation patches, while non-territorial males do not defend (Pajunen 1966; Convey 1988; Córdoba-Aguilar 2000). It has been shown that, compared with non-territorial males, territorial males are in better physiological condition, measured as muscle mass and/or energy reserves (Marden & Rollins 1994; Plaistow & Siva-Jothy 1996; Koskimäki et al. 2004; Contreras-Garduño et al. 2005). Both territorial and non-territorial males secure mating, but territorial males are more successful (Plaistow & Siva-Jothy 1996; Serrano-Meneses et al. 2007). Non-territorial males manage to copulate by sneaking when the territorial males are temporarily absent or away from territories intercepting female (Forsyth & Montgomerie 1987). It is known that a male may (or may not) alternate these two types of behaviour during his life. Preference for one of the tactics, or prevalence of one of them throughout life or at certain stages may depend on different factors, e.g., (1) genetically determined characteristics such as size and/or coloration (Siva-Jothy 1999; Koskimäki et al. 2009), (2) age (Forsyth & Montgomerie 1987; Plaistow & Siva-Jothy 1996), (3) energy reserves (Plaistow & Siva-Jothy 1996) or (4) external factors such as population density (Tsubaki & Ono 1986). Therefore damselflies are a good model organism for studying the relative importance of these determinants of male behaviour.

Most intensively studied in this respect are *Calopteryx* damselflies (reviewed in Córdoba-Aguilar & Cordero-Rivera 2005). This genus includes *ca* 20 Holarctic species (Misof et al. 2000). Sexually mature males spend their whole life at a riverside. In some places males aggregate with densities up to 2–3 active males per m². Females also occur here to copulate and lay eggs. Alternative mating tactics (territorial *vs* non-territorial males) of *Calopteryx* are known to be condition-dependent, governed by fat stores and/or age of the male (Forsyth & Montgomerie 1987; Plaistow & Siva-Jothy 1996; Contreras-Garduño et al. 2006). Usually territorial and non-territorial males do not differ in genetically determined characters like body size and/or coloration (Córdoba-Aguilar 1995; Plaistow & Siva-Jothy 1996; Sarfaty & Pruett-Jones 2010; but see Koskimäki et al. 2009 for an exception).

However, despite numerous studies (reviewed in Córdoba-Aguilar & Cordero-Rivera 2005), space use of damselflies is not known in detail. For instance, it is not known whether territorial males occupy a single territory or they can switch territories, whether territory borders are stable or can change with time (Chaput-Bardy et al. 2010). Even less information is available on behaviour of non-territorial males, which could hamper interpretation of the existing empirical data.

This paper describes and discusses the main aspects of space use of territorial and non-territorial male *Calopteryx splendens* (Harris, 1780) in the context of current knowledge of alternative mating tactics in the Calopterygidae.

Material and methods

Study area and species

The material was collected in the Vladimir Oblast, Russia, on the banks of the small river Tymba near the village of Mstyora (56°22.531' N, 41°56.490' E), about 300 km east of Moscow. The main observations were made on 1–18--vii-2012 and 24-vi–13-vii-2013. Preliminary data were collected in June and July 2010. The study plot was situated along the 20 m wide river and occupied an 85 m long section of the river.

Calopteryx splendens is common in Central and Southern Europe as well as the European part of Russia, and occurs near running waters with abundant aquatic vegetation, except in cold streams and shaded areas of rivers. On the Tyumba river it is the most common damselfly. Males of *C. splendens* are unevenly distributed across their typical habitats; although individuals may be encountered in any suitable area of the river, in certain parts males aggregate with densities up to 2–3 active males per m². One aggregation site was located within our study plot. The water was there partially covered by patches of Flowering rush *Butomus umbellatus*, the stems of which were used as perches. Both sexes occured here, copulating and with females ovipositing on submerged stalks of *B. umbellatus*.

In the Vladimir Oblast, *C. splendens* usually appears in June, with some annual variation according to the seasonal climatic conditions. Initially, almost exclusively males are present at the river and females appear only several days later. In August, *C. splendens* numbers begin to decline. However,

individuals do not survive throughout this period but are replaced by new individuals.

Basic field methods

Damselflies were captured with a butterfly net and marked by paint. A combination of marks was made on abdomen and wings. After marking, the insects were placed on plotting paper and photographed. On the basis of photographs we measured the wing length, from the base to the tip, to the nearest 0.1 mm using Adobe Photoshop CS4.

Observations and captures of damselflies in the study plot were performed daily for 2–4 hours. We treated the males that remained within a limited area not exceeding 0.5 m² throughout the observation period on a given day as territorial, while the remaining males were treated as non-territorial. Beyond space use, territorial and non-territorial males exhibited behavioural differences that were not clear cut. Territorial males tended to remain close to the water surface and defend a territory while non-territorial males usually perched on higher parts of the vegetation.

On 20-vi-2010 and 14-vi-2012, we performed two additional surveys of damselflies at a transect 700 m upstream of our study plot, which was completed at the border of the actual study plot. During these surveys, we tried to detect marked individuals.

The study plot, including all patches of flowering rush larger than 0.5 m², was mapped (Figs 2, 4). These patches were numbered, and during observations the respective patch number in which a male was observed, was noted (up to four patches in one day). Thus, each male during every day of observation was (1) characterized as either territorial or non-territorial and (2) mapped as present in a particular habitat patch.

Capture-mark-recapture models

Life expectation of damselflies after marking was estimated by stochastic capture-mark-recapture models (Cormack-Jolly-Seber models). In this case, only presence/absence of a male in the study plot on a given day was taken into account. Model selection was performed on the basis of Akaike's information criterion using the programmes Mark 5.1 and Mark 7.1 (WHITE & BURNHAM 1999).

The estimates of lifetime expectation were similar in both 2012 and 2013, *ca* six days (see below). Therefore in the subsequent analysis we used (with a single exception, see below) the data on males who were last recorded at least seven days after marking. We believe that material obtained from these males (a total of 43 males in 2012 and 2013) is representative.

Analyzing space use
Our marking method established male "age" from the date of male appearance at the stream. We analyzed the proportion of territorial males depending on male "age". A curve was fitted by the highest order polynomial regression that provided a significant improvement in the fit of the model.

During material processing, each male was characterised by three main parameters: (1) number of days elapsed since capture until the final encounter; (2) number of days when the male was recorded as territorial; (3) number of days when the male was recorded as non-territorial. Two additional parameters were the derivatives of these basic ones: (5) the duration of the territorial phase and (6) the duration of the non-territorial phase (see below).

We identify a territorial and a non-territorial phase in a male's life (see examples in Fig. 2). We define the territorial phase as all days since the first record of a male until the last record as a territorial individual. The remaining days are defined as the non-territorial phase. If a male had never been recorded as territorial, we treat all observations of this particular male as referring to the non-territorial phase.

We tested whether spatial tactic (territorial *vs* non-territorial) of males on day $n+1$ depends on their tactic on day n. To this end, we built a transition matrix, which contained the number of observed transitions between different spatial tactics in consecutive days (Table 1). The probability of occurrence of the tactic used on day $n+1$ was the same as used on day n was tested using Fisher's exact two-tailed test.

It is known that different territories, i.e., vegetation patches, differ by their attractiveness for males: some are only occasionally occupied whereas other are always occupied. Moreover, the patches more attractive for males are more often visited by females who copulate with the local males (GOLĄB et al. 2013; PANOV & OPAEV 2013). As a proxy for attractiveness of a given

patch we used the overall number of individually marked males pooled for all observation days. In this case we included all marked males, and not just the ones that were recorded for at least seven days.

For the analysis of spatial behaviour of males in a non-territorial phase, we used only the cases when the male was recorded on at least two consecutive days. For each such case we noted (1) whether the focal male was recorded in day $n + 1$ in at least one of the patches where he was observed in day n (yes/no); (2) the maximum distance between his locations in days n and $n + 1$.

Home ranges of damselflies were mapped. The main parameter was the distance along the river between the centres of the most distant patches of flowering rush visited by the particular male. When the male was only recorded in a single patch, its home range size was not estimated (4 males out of 43).

Statistical analysis

Most variables mentioned above showed normal distribution (Kolmogorov-Smirnov test, $p > 0.05$), therefore to compare different variables we used parametric tests (Student's t-test, Pearson correlation, Chi-square test). In one case, when the size of one of the samples was below 8, we used non-parameteric Kruskal-Wallis ANOVA. In another case, when one of the samples significantly deviated from the normal distribution (Kolmogorov-Smirnov test, $p < 0.05$), we used Spearman's rank order correlation. No variables showed significant difference between the two years of study, 2012 and 2013 (Student's t-test, $p > 0.05$), therefore the data were pooled across both years.

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Results

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Lifetime expectation of males and females after marking

In 2012, we captured and marked 106 males and 34 females; in 2013, 97 males and 22 females. In the subsequent days we re-encountered 70 males (66.0 % of marked males) and 11 females (32.4 %) in 2012, and 68 males (70.1 %) and four females (9.1 %) in 2013.

The 2012 data were best fitted by the time-independent apparent daily survival and time-dependent daily re-encounter probability (Akaike weight 0.684). The model contained no sex structure. Daily apparent survival estimate was 0.861 (95 % confidence interval [CI] 0.833–0.885). The expected

lifespan after marking calculated from these apparent survival estimates was 6.68 days (95 % CI 5.47–8.19 days). In 2013, a sufficient dataset was only available for males. Most support was received by two models (Akaike weights 0.58 and 0.41, respectively), both with time-since-marking-dependent apparent survival estimates that provide differences between the first day after marking and all subsequent days. In the best model, survival from the day of marking to the subsequent day was 0.992, and survival in the subsequent days was 0.813 (95 % CI 0.764–0.853). These estimates result in the lifetime expectation after marking of 5.83 days (95 % CI 4.71–7.29 days).

The maximum recorded lifespan of a male after marking was 19 days. In addition, on five occasions, we recorded dead males without apparent injuries that had probably died of natural causes. In all cases those males must have died on the day of observation because dead bodies were quickly taken away by the current. Two of these five males had been marked eight and two days before.

Home range size in males

Male home range was on average 29.6 ± 12.2 m along the river (range 11–56 m, $n = 39$) and therefore smaller than our study plot (85 m). This is further confirmed by the two additional surveys performed at a 700 m transect upstream from our study plot. Only once in 2010, we recorded one marked male 50 m from the study plot. Within the study plot, six and 17 marked males were recorded during the surveys in 2012 and 2013, respectively.

Lifetime dynamics of male spatial behaviour

The probability that a given male is territorial declines during its life: the proportion of territorial males in both years of study decreased after the first day of marking (Fig. 1). The regression for the proportion of territorial males was linear (first order polynomial): $r = -0.89$, $p < 0.01$, $y = 0.74 - 0.05 \times x$.

The occurrence on day $n + 1$ of the same tactic that was used on day n was significantly higher than the alternative tactic (Fisher's exact two-tailed test, $p < 0.001$; Table 1). Thus, the spatial tactic of males is temporally autocorrelated. We therefore identify a territorial and a non-territorial phase in a male's life. The duration of these two phases in days is roughly equal: on average *ca* seven days, up to maximally 15–16 days (see below for details).
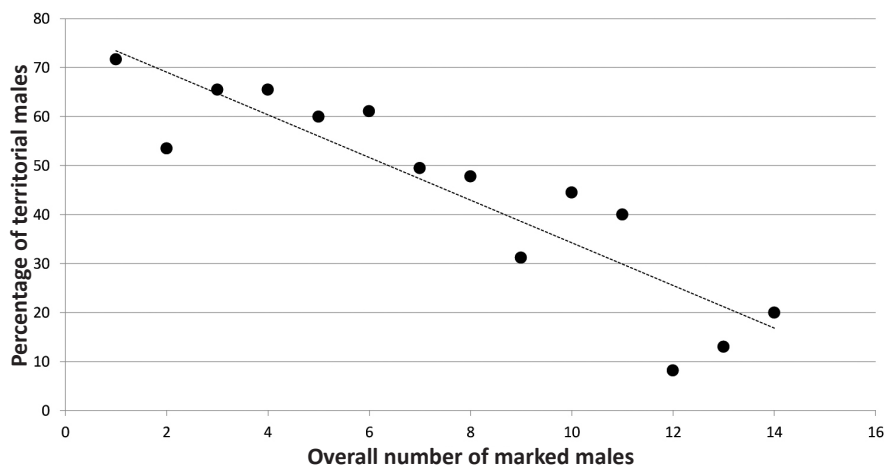
Table 1. Number of observed transitions between different spatial tactics in consecutive days, of individually marked *Calopteryx splendens* during the summers of 2012 and 2013, on river Tymba near the village of Mstyora, Vladimir Oblast, Russia. The observed probabilities are given in parentheses.

day *n+1* / day *n*	Territorial	Non-territorial
Territorial	95 (0.83)	25 (0.29)
Non-territorial	19 (0.17)	61 (0.71)

Territorial phase in male's life

The territorial phase was recorded in 28 males of our sample (65%, $n = 43$). Ten of them were only observed as territorial males, and the remaining ones in both phases.

Most territorial males were captured within their territory and were observed as territorial individuals on the day of capture (64%: 18 out of 28). Of the remaining males, eight were recorded in the study plot as vagrants before they had occupied a territory. Two more males were observed as ter-

Figure 1. Percentage of territorial males of individually marked *Calopteryx splendens* during the summers of 2012 and 2013, on river Tymba near the village of Mstyora, Vladimir Oblast, Russia, as a function of day since marking.

ritorial several days after capture and were not seen in between. Time lag between capture and the occupation of a territory for the 10 territorial males was 2.2 ± 1.2 days (range 1–5 days).

The duration of the territorial phase was on average 6.9 ± 3.4 days ($n = 28$), with a maximum of 16 days. During this phase, a male may follow one of the three variants of spatial behaviour. According to our observations, he may (I) occupy a single territory; (II) be non-territorial in some of the days, and then return to his previous territory – e.g., male 1 (2013) and male 12 (2013) in Figure 2; or (III) after staying within a certain territory for several days change it and occupy another territory on the next day for several days – e.g., as male 46 (2012) in Figure 2. In variant III, the number of such territories may be 2 or 3, on average 2.4 ($n = 10$). The distance between the subsequently occupied territories was on average 13.5 ± 5.9 m (range 4.7–25.0 m, $n = 14$).

Variant I was the most frequent observed and was recorded in 13 males (46 %), variant II in 5 males (18 %), and variant III in 10 males (36 %). Males that practiced these strategies did not differ by (1) the duration of the territorial phase and (2) the number of days during which they were recorded as territorial (Kruskal-Wallis ANOVA, $p > 0.05$). However, the number of days spent in the first territory, differed (Kruskal-Wallis ANOVA, $p = 0.011$, significant with Bonferroni correction). Therefore, during the same period, a male may remain within a single territory or subsequently occupy different territories.

Our data revealed an inverse correlation between patch attractiveness and the median duration of stay of males on a given perch (2012: $R = -0.97$, $p = 0.005$; 2013: $R = -0.97$, $p = 0.005$, and for the pooled sample in Figure 3: $R = -0.97$, $p < 0.001$). Therefore, territorial males remain on average for a smaller number of successive days on patches that are generally better attended (Fig. 4).

Non-territorial phase in male's life

The non-territorial phase has been recorded in 34 males from our sample (79 %). Of them 15 individuals were only observed as non-territorial. The duration of non-territorial phase was 7.6 ± 3.4 days ($n = 34$), range 1–15 days. Of this period, the increased mobility of males is characteristic. In the
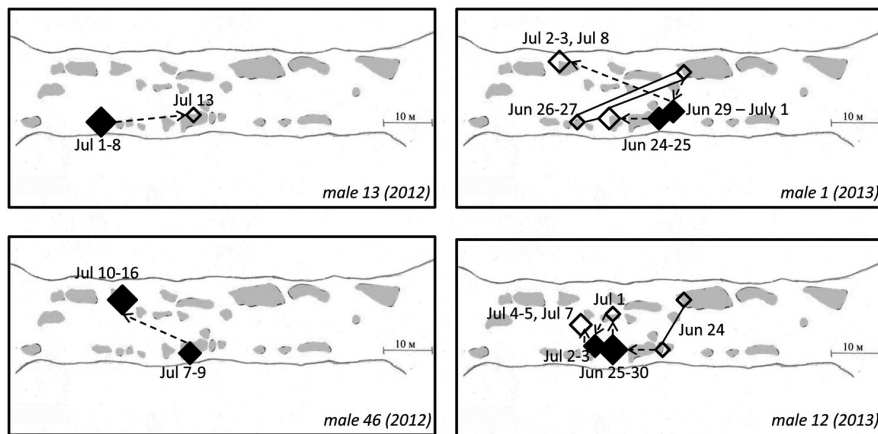
Figure 2. Examples of spatial behaviour of male *Calopteryx splendens* during the summers of 2012 and 2013, on river Tymba near the village of Mstyora, Vladimir Oblast, Russia. ◆ – males territorial on a given day; ◇ – non-territorial males. Diamond size is proportional to the number of days spent in a particular location (dates are shown). Broken lines connect locations of males in consecutive days; solid lines connect locations within the same day.
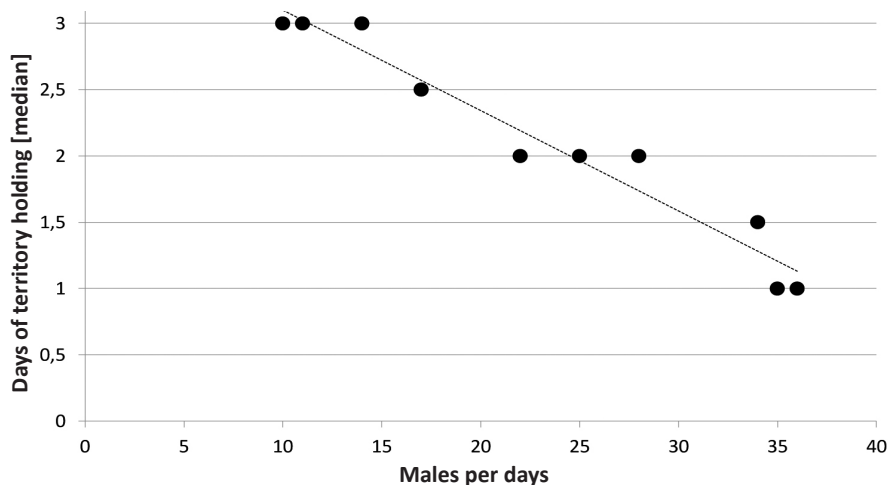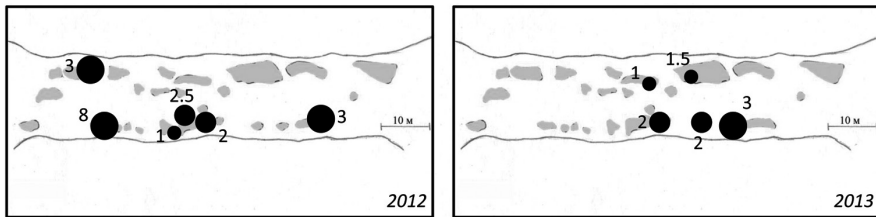

Figure 3. Relationship between duration of territory holding and presence at a vegetation patch by marked male *Calopteryx splendens*, during the summers of 2012 and 2013, on river Tymba near the village of Mstyora, Vladimir Oblast, Russia.

non-territorial phase the males move around within their home range and are not confined to certain vegetation patches, i.e., territories.

Of 15 males recorded in their non-territorial phase, just nine were recorded at least once in two consecutive days. Usually a male which abandons his territory is still regularly recorded in its vicinity or within the territory itself during 1–3 days. In the first 3–4 days after becoming non-territorial the maximum distance between record locations in consecutive days is small (Fig. 5a), and afterwards it starts to increase. The minimum distance on the third day illustrates another noteworthy pattern of declining territorial activity. Some males after abandoning their territory move to one of the adjacent habitat patches. At this new patch the damselfly behaves as a non-territorial individual and is present only periodically. However, its presence here is regular, which contrasts with the lack of records in other portions of the focal area. A similar, albeit less pronounced, trend is apparent in the daily dynamics of the proportion of males that are not recorded on consecutive days at the same patch (Fig. 5b). Therefore, territorial status of formerly territorial males declines with time and former territorial males show declining site fidelity.

Taking the mobility of males in the non-territorial phase into account, one can expect that the size of their home range will be related to the number of days of observation. This relationship, albeit not very strong, is indeed observed: Pearson correlation coefficient $r = 0.39$, $p = 0.015$ ($n = 39$).

Non-territorial males were often involved in flights with other males and chased females, which could result in copulations. However, our impres-

Figure 4. Distribution of habitat patches and duration of territory holding by marked *Calopteryx splendens* males during the summers of 2012 and 2013, on river Tymba near the village of Mstyora, Vladimir Oblast, Russia. The figures show the median duration of territory holding. Dot size is proportional and smaller dots denote more attractive patches (see text and Fig. 3).
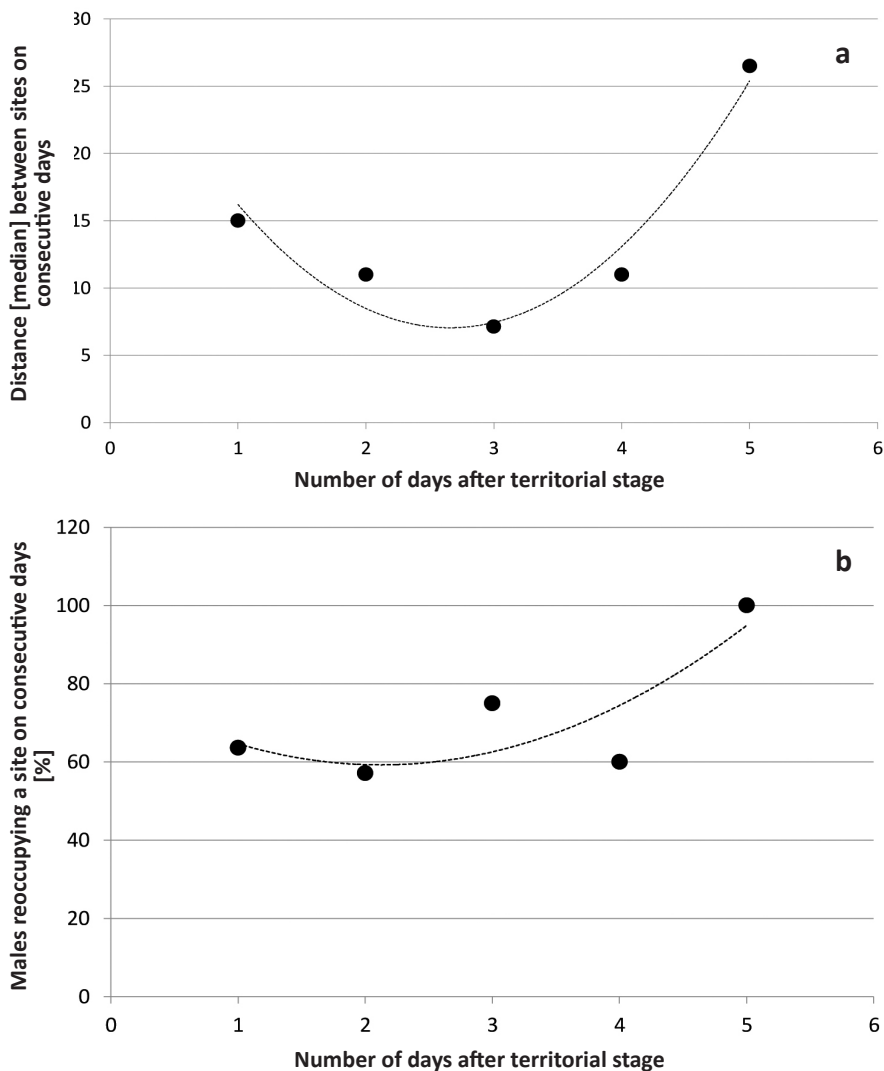
Figure 5. Spatial behaviour of male *Calopteryx splendens* in the first five days of the non-territorial phase. a – median value of maximum distances [m] between patches used by a male on consecutive days; b – percentage of males that on a given day were recorded at least once at the same patch as on the previous day. The X-axis shows the number of days since the end of the territorial phase; the last day of the territorial phase (day 0) is not shown. The number of observations (*n*) for each day is equal for both parameters.

sion was that this activity gradually declines with age of the individual. Our observations show that the oldest males can be identified by the colour of their wings, which gradually become duller and more greenish with age. We have frequently observed such individuals sitting on the upper parts of stalks, where they are inactive and pay no attention to other damselflies, either males or females.

The role of roosting aggregations in the life of *Calopteryx splendens*
A typical feature of behaviour was roosting aggregations in the riparian vegetation, the 1–2 m wide grassy stripe along the river bank. In these roosts, the distance between the individuals may be as small as a few centimetres. Roosting damselflies are clumped in certain areas, which suggests that they actively gather into such groups. One or two hours after sunrise, when the damselflies are warm, they distribute themselves across the study area and occupy plant stalks above the water.

Apart from the roosts, some aggregations may also be observed in the daytime. They usually do not include more than 10 individuals that remain on riparian vegetation or in vegetation patches not far (1–2 m) from the bank. The distance between sitting damselflies may be *ca* 10 cm or even less. Males in such groups may sit in close proximity and from time to time engage in mutual flights. Of such groups, the following features are characteristic: (1) they only include non-territorial males; (2) damselflies often sit on the upper parts of stalks, which is typical of individuals weakly involved in social interactions; (3) even though these aggregations may be observed at any time of day, they are commonly formed in the afternoon (15:00–16:00 h MSK (UTC+3) in July, whereas the typical roosting aggregation do not form until after 18:00–19:00 h).

Individual lifetime trajectories and wing size
The wing length was 32.2 ± 1.2 mm (range 29.9–35.7 mm, $n = 42$). Wing length did not correlate with (1) number of days elapsed since capture until the final encounter; (2) number of days when the male was recorded as territorial; (3) number of days when the male was recorded as non-territorial; (4) duration of the territorial phase; (5) duration of the territorial phase and (6) home range size (Pearson correlation, $p > 0.05$).

Spatial behaviour and home range size of females

The available data on females are fragmentary. On two different, consecutive days we observed just one female (on 02- and 03-vii-2012). The distance between observation locations was 35 m. In another case, a female was recorded at two locations 20 m apart within the same day.

Females not looking for a partner and/or an area for laying eggs often spend time in a roosting aggregation. Aggregations involving females usually form in the riparian vegetation or on the trees growing near the river bank. Socially inactive males may also be present. Unlike the aggregations of non-territorial males, no interactions between damselflies are recorded in such groups. In this respect these groups are similar to communal roosts.

Discussion

In this study we describe the space use of *Calopteryx splendens* during the reproductive period. Our data indicate that the species can be observed from June until August, after which numbers start to decline. Similar phenology has been reported for other *Calopteryx* species, e.g., by Forsyth & Montgomerie (1987) for *Calopteryx maculata* (Palisot de Beauvois, 1805). However, particular individuals are not present throughout this period; new damselflies appear and former residents disappear. Male *C. splendens* have been reported to have a lifespan of 3–6 weeks (Chaput-Bardy et al. 2010). Our data are in general agreement with this estimate. For instance, the maximum recorded lifespan of a male after marking was 19 days. But the average expected lifespan after marking was *ca* six days. Our data on daily apparent survival estimates closely agree with the data obtained from the same species in France (Chaput-Bardy et al. 2010).

During their life, males used a home range, which was 11–56 m along the river. This observation is in good agreement with other data in the literature that suggest that the home range of a male usually does not exceed 50 m along the bank, and 80 % of males are never recorded farther than 100 m from the capture site (Stettmer 1996; Ward & Mill 2007).

Use of the home range depends on the male's tactics. Two types of behaviour, territorial and non-territorial, are distinguished. We treated as territorial the males that remained within a limited area not exceeding 0.5 m² throughout the observation period (2–3 hours) on a given day. The remain-

ing males were treated as non-territorial. A male may (or may not) alternate between these two types of behaviour during his life. Previous work has shown that the probability of a male being territorial is inversely age-dependent in *Calopteryx* (Forsyth & Montgomerie 1987). Our data suggest that a male has a high probability of being territorial during several consecutive days in the initial part of his life, and non-territorial (also during several days) in the final part. Thus, the territorial tactics in *C. splendens* is age-dependent. We identify a territorial and a non-territorial phase in a male's life, which occur consecutively. The duration of these two phases in days is roughly equal: on average *ca* seven days, up to 15–16 days. Considering that lifespan of a male does not exceed 3–6 weeks (see above), we can assume that, if a male survives that long, its adult life consists of a territorial and a non-territorial phase of roughly the same duration.

The probability that a given male is territorial declines during its life. The same tendency has been shown for *C. maculata* (Forsyth & Montgomerie 1987) and seems to be a general rule for damselflies. The reason behind this pattern is related to progressive depletion of fat stores with age, which has been shown for *C. xanthostoma* (Charpentier, 1825) (Plaistow & Siva-Jothy 1996). Thus, at some point older and/or more exhausted males begin to be unable to compete for a territory and become non-territorial.

The adult life of *C. splendens* consists of two stages, the pre-reproductive and the reproductive one (Corbet 1999). During these two stages, they occupy spatially distinct ranges. After emerging, adult damselflies leave the water and move several hundred metres away. As shown in *C. maculata*, they spend time in forest habitats and intensively forage. The duration of the pre-reproductive stage in *C. maculata* is *ca* one week (Kirkton & Schultz 2001). After that, damselflies return to the water body where reproductive sites are located. We found a time lag between capture and the occupation of a territory in 10 out of 28 males, which we observed during their territorial phase. The time lag between arriving at a reproductive site and territory occupation means that males are prevented from occupying a territory immediately upon arrival due to competition with rivals. This hypothesis is confirmed by our observations of five out of eight males for which we have data on this period in their life. Each male, before he occupied a territory, was recorded in the vicinity

of his future territory for 1–2 days. During this period, we recorded mutual fluttering flights with other damselflies inhabiting this area. These flights are known to result in the expulsion of one male by the other (Pajunen 1966; Panov & Opaev 2013). The three other males were not recorded in the immediate vicinity of their future territory in the preceding days.

We found that during the territorial phase of their life a male can change territories (i.e., perches) two or three times. We found that, on average, territorial males remain for a smaller number of successive days on perches that are generally better attended by other males. This suggests that territory change is mainly caused by competitive exclusion of males.

Based on our two data sets, we believe that competition with other males influences (1) the number of days when the male was territorial and (2) the number of territories he occupied. When male density is high, competition for territories becomes harder (e.g., Córdoba-Aguilar 2009; Córdoba-Aguilar & González-Tokman 2014). Thus, it is likely that variables (1) and (2) are density dependent. A relationship between population density and the percentage of territorial males has been found in other damselfly species (Tsubaki & Ono 1986; Suhonen et al. 2008).

However, the length of the territorial/non-territorial phases is not related to variables (1) and (2) and, therefore, may be less dependent on population density. Therefore, the length of the territorial phase may be more dependent on individual characteristics of the male in question than the number of days it is territorial. We found there was a gradual transition from the territorial to the non-territorial phase and that this transition was related to 'ageing' rather than competition, as outcompeted males usually switched territory, although a combination of these two possibilities cannot be ruled out.

Larger males probably have an advantage in competition for territories and were therefore recorded as territorial more often. Moreover, larger males may remain territorial for a longer period of time, resulting in territory owners being larger than non-territorial conspecifics, however, this cannot be assumed to be a general rule. For instance, although data from Koskimäki et al. (2009) appeared to show that, in Finland, 'territorial' male *Calopteryx virgo* (Linnaeus, 1758) were larger than 'wandering' conspecifics, the criteria they used to assign males to territorial or non-territorial groups were unsatisfactory (Panov & Opaev 2013: 812).

We, therefore, suggest that further studies on variation in spatial and sexual behaviour of damselflies should focus not on the formal comparisons of phenotypes, but rather on comparing the fates of individual males, and particularly the duration of territorial and non-territorial phases. Only then should morphology and activity be brought into the equation. Our study did not show any correlations between the size of males and their life trajectories.

Although the study by Beck & Pruett-Jones (2002) appeared to show that large male *C. virgo* retain territories for a longer period and have a longer lifespan, the non-territorial status was assigned *a priori*. Beck & Pruett-Jones (2002: 782) write: »we collected non-territorial males at random ... Non-territorial males were identified as those up to 3-m inland that showed none of the behaviors typical of territorial males«. It should be emphasized that »these were the individuals that showed none of the behaviors typical of territorial males« at the moment of capture.

In a study on *Hetaerina americana* (Fabricius, 1798), each male was observed for 15 min to allowing assessment of a male's territorial status. This study showed that the number of days a male held a territory increased with body length (Serrano-Meneses et al. 2007). However, unlike *Calopteryx*, territorial status in *Hetaerina* does not depend on male age and, therefore, does not change during their life (Córdoba-Aguilar & González-Tokman 2014). Therefore, in *Hetaerina* the male's status on any given day clearly reflects his lifetime trajectory. This is not the case in *Calopteryx*, because males move from territorial to non-territorial phases as they age and the transition from one to another is gradual.

Summarizing, we suggest that studies of alternate mating tactics in *Calopteryx* are incomplete unless the length of an individual's territorial and non-territorial phases are included.

Acknowledgments

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