ORIGINAL PAPER



Telemetry reveals the habitat selected by immature dragonflies: implications for conservation of the threatened dragonfly *Leucorrhinia caudalis* (Odonata: Anisoptera)

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Received: 28 July 2018 / Accepted: 20 December 2018 © Springer Nature Switzerland AG 2019

Abstract

Determining how species use different habitats during critical phases of their development is one of the crucial challenges that conservation biology meets. However, habitat requirements remain unknown for most species, in particular for the rarest and most threatened which by definition are difficult to study. Here, we used animal-borne telemetry to identify the habitat of the sexually immature adults in the threatened dragonfly *Leucorrhinia caudalis*. We used an harmonic radar with customized tags fixed on the back of the abdomen of flying immature dragonflies to monitor their position within an area composed of various types of habitats including open areas, forest and water bodies. From 62 tagged individuals, we obtained 23 detections, all within a quite restricted area around the pond of emergence. About 75% of the detections happened in the forest canopy and the individuals were likely positioned at the top of the trees. The relatively low detection rate was probably due to high predation within the study area during the maturation phase in this dragonfly but long-range dispersal cannot be excluded. The use of forest canopy as a maturation habitat is an important knowledge for planning conservation strategies in this endangered species, especially for populations living in areas without any protection status. Although technological constraints are still limiting its efficiency, animal-borne telemetry appears to be useful to determine precisely habitat selection by rare species.

Keywords Harmonic radar · Displacements · Dragonflies · Spatial ecology · Maturation · Endangered species

Introduction

Human activities bring many threats to both terrestrial and aquatic biodiversity (Scheffers et al. 2016) leading to the sixth mass extinction (Ceballos et al. 2015). Conservation plans have been developed in many countries to minimize biodiversity losses (Rands et al. 2010). To be efficient, those plans need to be supported by precise ecological knowledge

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10841-018-00123-9) contains supplementary material, which is available to authorized users.

on life history traits of species (Balmford and Cowling 2006) but habitat requirements still remain to be determined for most species. This is especially crucial for threatened species, which are often rare and difficult to study.

In this context, about a quarter of the European dragonflies (Odonata) have declining populations (Kalkman et al. 2010) mostly due to habitat loss and/or intensive land use (Merritt et al. 1996; Samways 1996). Habitat requirements of dragonflies are highly species-specific (Watson et al. 1982). They are relatively difficult to determine as Odonata species exhibit complex life cycles, shifting from aquatic to terrestrial habitats, thus crossing ecosystem boundaries (Knight et al. 2005). Most species spend major part of their life in the larval stage in aquatic habitats and conservation studies have mostly focused on those aquatic habitats (Samways 2008). Yet, terrestrial landscapes may also play an important element limiting species presence (Rouquette and Thompson 2007; Dolný et al. 2012; Hykel et al. 2016). Responses to a stressful environment at any stage may carry over and shape fitness in subsequent stages and generations

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(Stoks and Córdoba-Aguilar 2012). The ecology of sexually mature individuals has received some attention (e.g., Corbet 1980; McPeek 2008) but comparatively little is known on the behaviour and requirements of individuals during the maturation period (e.g., Parr 1983; Anholt 1990; Corbet 1999, pp. 271-273; Hardersen 2007). During this period (several days to weeks), immature individuals move between aquatic and terrestrial habitats. The habitats used during this stage are often loosely described in the literature, referring in most cases to "individuals staying in the vegetation" (e.g., Corbet 1957, 1980) or "associated with woodland and canopy" (e.g., Pajunen 1962; Corbet 1999, pp. 271–272; Ha et al. 2002). A precise description of the habitats used by dragonflies during this critical maturation period should help determine their exact trophic position in terrestrial ecosystems and therefore to improve conservation plans (Foster and Soluk 2006).

The use of animal-borne telemetry has improved considerably our understanding of species' ecology and it was proved helpful to inform conservation practices (Cant et al. 2005; Kays et al. 2015; McGowan et al. 2017). Techniques such as radio telemetry have been used for more than 50 years for studying individual movements, habitat use, and dispersal of animals (Cochran and Lord 1963; Craighead and Craighead 1963; Millspaugh and Marzluff 2001). Transmitters used in radio telemetry are powered by batteries, contributing to their weight and making them unsuitable for most insect species. As an alternative, passive tags do not need power source and hence can be reduced to a fraction of the weight of active transmitters. Since the 80s, such technique of harmonic radar was used to study movement and space use of flying insects (Mascanzoni and Wallin 1986; Hardersen 2007). This approach uses a small passive transponder attached to the insect that sends back transmissions at exactly half the wavelength of the original transmitted wave. The miniaturization of telemetry systems started during the 1990s (Naef-Daenzer 2005), making possible to follow insects with body weight down to 150 mg (e.g., butterflies: Cant et al. 2005).

Here, we determined the habitat selected by the dragonfly *Leucorrhinia caudalis* (Charpentier, 1840) during its maturation stage. *L. caudalis* is a threatened dragonfly species in Europe (Sahlén 2006). Although its IUCN status was recently lowered to Nearly Threatened (NT) for Europe, the status stands as Endangered (EN) for the region Centre Val de Loire (Sansault and Lett 2012). This species is both listed by the European Habitat Directive (Council Directive 92/43/EEC of 21 May 1992) and included in national conservation actions in France (Dupont 2010; Baeta et al. 2012a, b). This species is suspected to remain under the forest tree cover during the maturation period because it was never observed in open areas (Courant and Même-Lafond 2011), but this habitat use remains to be directly identified. To follow the displacements of individuals during their maturation in the field, we used a RECCO[®] harmonic radar system derived from a commercial portable avalanche rescue system associated with very small customized tags fixed on the back of the abdomen of individuals collected upon emergence. We equipped a large number of individuals, which is not often the case with telemetric studies. This system was already successfully applied to a small number of adult dragonflies immediately after emergence (Hardersen 2007) but this technology was never used with clear conservation purposes on a threatened species.

Materials and methods

Study species and study site

In France, L. caudalis reaches the western and southern edges of its distribution, with higher population densities in the center, east and north-east of the country. Populations have declined in the last decades but a recovery is observed since the 2000s throughout its range, with new populations discovered in the western part of the range (Kúdela et al. 2004; Jović et al. 2008; Muusse and Veurink 2011; Sansault 2011; Baeta et al. 2012a, b; Kulijer and Miljević 2015). It is not clear, however, if this apparent recovery is linked to a change in sampling rate (more observer going more often on more sites) or to environmental changes. Aquatic habitats are mostly mesotrophic to weakly eutrophic lakes or bogs with clear water and rich submerged and floating vegetation (Kalkman and Sahlen 2015). The flight period is from April to July depending on the local climate (Dupont 2010). Mature males move mainly for the defense of the territory, and mature females for finding places to lay eggs (Grand and Boudot 2007; Dijkstra and Lewington 2007). Keller et al. (2010) highlighted the very low dispersal rate of this species. The duration of the immature stage is about 10 days (Grand and Boudot 2007; Dupont 2010).

The study area is located in France, in the Centre-Loire Valley region, inside the forest of Tours-Preuilly. This (managed) forest is composed of hardwood and coniferous lots, wetlands and grasslands. The study site is a 1 km radius circle centered on a 0.3 ha pond, known for the high density of *L. caudalis* ("La Rolle", 46°52′29.7"N 1°00′49.9"E) (Fig. 1) (Baeta et al. 2012a, b). In 2015, the study site was composed of deciduous forest (68%), coniferous forest (20%) and heath (7%); see Fig. 1. The vegetation surrounding the pond was composed of woody, shrubby and herbaceous stratums. In the pond itself, aquatic vegetation was well developed with helophytes such as *Iris pseudacorus* and *Myriophyllum spicatum*.



Fig. 1 Distribution of the various types of habitats within the 1 km radius study site (**a**) and zoom of the detection zone (red polygon) around the pond, which comprised all the detections (**b**). The white dots indicate the individuals that were not identified (11 detections) and each colored dot shows the position of the identified individu-

als (five identified individuals; one has two points on the map). The crosses show the position of the dead individuals (N=6). The black star indicates the location where individuals were released. No tagged individual was detected outside this maturation zone within the study site. (Color figure online)

The telemetry system

The avalanche rescue system RECCO® was used to follow L. caudalis during its maturation period. This passive system uses very light battery-free tags to follow small organisms. The RECCO[®] transmitter emits a 1.5 W continuous harmonic frequency at 917 MHz. The tag reflects a signal at twice this frequency (1834 MHz). Each tag is composed by a Schottky diode (D-1 model provided by RECCO AB, Lidingö, Sweden) and a dipole antenna made from one piece of ca. 20 cm of enamelled copper wire (3.2 µm in diameter; SX0032-050, wires.co.uk, England). The wire is welded to each diode poles so that each tag pole is 8 cm in length and a loop of 30 mm is left between the anode and the cathode to prevent electrostatic charges (Hardersen 2007). The tag, including the glue (see below), weights 16.5 ± 1.5 mg (mean \pm SD, N = 7; measured with OHAUS PA64 Pioneer Analytical Balance). The maximum detection distance in an open area was 117.9 ± 17.3 m (mean \pm SD, N = 12).

Application of the system in the field

Freshly emerged individuals (often called tenerals) were captured by hand during the mornings of May 12th and 13th 2015, under sunny and calm weather conditions. They were maintained for 4 h inside a large mosquito tent, with branches to serve as perches, to allow them to spread their wings and initiate their first flight in a large space. Once the wings were well spread out and dry, individuals received the tag in a dark and relatively cool room (20-24 °C) near the pond. The body mass of each individual in a subsample was measured with a calibrated scale (precision: 1.11 mg; OHAUS PA64 Pioneer Analytical Balance) to make sure the tag did not exceed 10% of the body mass (Table 1). The body mass of mature individuals was also measured few weeks later as a comparison (Table 1). These mature individuals were caught with a butterfly net while flying over the pond (they were different individuals than those equipped with the tag system).

Table 1	Mean $(\pm SD)$	body mass	(mg) of	immature	and ma	uture ind
viduals	of L. caudalis					

	Mean body mass (mg) ^a	SD	N
Immature (total)	164.59	18.09	14
Males	165.71	18.59	7
Females	163.46	17.84	7
Mature (total)	196.47	34.05	17
Males	182.95	14.82	14
Females	259.58	26.19	3

^aThe weight of each individual was the average of four successive measures

To apply the tags, individuals were maintained on a setting board with the wings open (Fig. 2). A drop of Cyanoacrylate glue (Loctite Super Glue 3 Precision) was applied at the base of the diode and left for few minutes since the glue needs to slightly dry up before application. The tag was positioned dorsally on the third abdominal segment in the length of the body and held in place for 30 s. Short drying time reduces manipulation stress. After fixation, individuals were replaced in the tent on a perch. The type of tags and transmitter used in this study do not allow individual differentiation. Therefore, wing marking was used to discriminate visually among the individuals (Fig. 2). A simple alphanumerical code composed of one capital letter and one number was written with a black pencil (STAEDLER Lumocolor) on the underside of the two posterior wings.

Tagged immature individuals were released on the same day of emergence, ca. 6 h after capture (N=62 individuals). They were released in an open area in the middle of the study

site, less than 20 m from the pond (Fig. 1). After taking off, each dragonfly was followed with binoculars until it landed. The approximate distance (estimated with a tape measure after we memorized the path by eye), time (measured with a stopwatch) and direction (inferred from a compass) of the first flight were noted for a subsample of 37 individuals. We estimated the potential influence of the tag system on the flying ability by comparing the first flight performance of immature individuals equipped with the tag system (N = 33individuals) versus untagged immature individuals (N=4individuals) which received the same manipulations than before from capture to release, but without the application of a tag. The flight distance was compared to estimate how far individuals flew with the tag, while the speed of first flight was compared to analyze the ability to fly with the tag. In general, individuals (both equipped and untagged) had a relatively linear trajectory during this first flight, without any looping or convoluted behaviors.

During the period of May 15–26, 2015, corresponding to the maturation delay (~10 days), individuals were searched inside the study area (1 km radius). Monitoring was organized every day, depending on weather conditions, during the first week of the period and every 2 days during the second week. Two RECCO[®] transmitters were used by two teams (composed of the same persons all time) to scan the entire study site. During monitoring, the two teams covered distant areas to increase the probability to encounter tagged individuals. The monitoring occurred along transects following (i) the forest tracks, (ii) the forest edges, (iii) the periphery of the different water bodies and (iv) at the heart of several forest lots. A total of 35 km were walked within the 1 km radius area. Transects were defined by the tracks crossing the forest



Fig. 2 Illustration of two immature individuals equipped with the diode system. Individuals were marked on the wings to identify them when they were detected. Photographs: Eric Sansault



Fig. 3 Path of the transects used to detect tagged *L. caudalis* individuals during the study period. The shaded area around transects indicates the maximal detection distance (118 m) on each side of each transect

lots (Fig. 3). As much as possible, we deviated from the tracks to enter forest lots and to increase the global coverage. Every day of monitoring, different transects both close and remote from the focal pond were walked (with some overlapping). Due to battery limitations, it was impossible to cover the entire study site in a single day even with two teams but each transect was repeated at least twice across the study period. The transmitter was used continuously while walking along transects: it was moved from right to left and up and down permanently (frequency: one way right-left or one way up-down every ~ 4 s) to ensure that the directional signal transmits and receives in all directions. This way of handling the transmitter increases the probability to detect a moving target. For every contact (i.e., individual detection), the following parameters were recorded: the GPS coordinates, the individual code on the wings when visible, date, time and habitat (type of vegetation, tree species, height). Dead individuals were collected when we encountered them. They were discarded from the displacement analysis because these individuals may have been displaced by predators for example (but see "Discussion"). We also discarded the first 2 days of monitoring from the analysis to limit the potential impact of hand manipulation of the individuals and of releasing them at the same location.

Statistical analyses

Geographical analyses were conducted using QGis (2.4). We mapped the study area from aerial photographs (IGN BD ORTHO[®] 5 m 2011) and used field notes (to update landscape composition in some lots). A Student's *t* test was used to test for the difference in body mass between the

Table 2 Influence of the tag system on the mean $(\pm SD)$ speed $(m s^{-1})$ and distance (m) of first flight of equipped and free individuals of *L. caudalis*

	Without tag	With tag	
N	4	33	
Mean speed (m s^{-1})	1.85 ± 0.26	1.91 ± 0.56	
Mean distance (m)	22.55 ± 11.09	22.58 ± 7.60	

sexes. An exact multinomial goodness-of-fit test (function *xmulti*, package *XNomial* version 1.0.4) was performed in R 3.2.3 (R Development Core Team 2013) to determine if the observed distribution of immature individuals in each habitat differed from the theoretical distribution, i.e., equally distributed among all habitats, weighted by the total area of each type of habitat within the detection zone which was determined using MCP100% (Minimum Convex Polygon) on QGis.

Results

Mature females were apparently heavier than mature males, although only three mature females were captured (Table 1; no statistical test was done due to this low sampling size). This difference was not observed in immature individuals. The body mass of males and females upon emergence was similar (Student's *t* test: $t_{12} = -0.22$, p = 0.83) (Table 1). On average, the tag system corresponded to 10% of the body mass of immatures. The tag system did not influence the speed of first flight (Student's t test: $t_{35} = -0.21$, p=0.83; Table 2) nor its distance (Student's t test: $t_{35} = -0.01$, p = 0.99; Table 2). A total of 35 km were walked across the study site with the radar system. Assuming a single linear transect 35 km long and a detection distance of 118 m on the two sides of the transect, we estimate that our approach covered 8.5 km² at the end of the study period (the study site is 3.14 km²). Every day, between 27% and 39% of the total study area was sampled (Table S1).

A total of 23 contacts occured during the monitoring period. Among the 62 individuals that were equipped with the tag, 11 individuals were clearly identified, of which five were alive and six were dead, found on the ground using the radar system (Fig. 1). The five individuals alive were resting on plant materials when they were detected, at a distance of about 15–40 m. One of the living individuals was detected twice at two different locations. Eleven contacts were not identified because the code was impossible to read, however the sound signal of the RECCO indicated unambiguously the direction of the top of the canopy (at a distance of roughly 20–40 m). Most of the contacts occurred within the first 6 days of the study period (Fig. S1). The detection



Fig. 4 Proportions (%) of habitat in the detection zone and proportions of individuals detected by the RECCO[®] system in these different habitats

zone of immature individuals that were detected was mostly composed of forest, water and open habitats. The proportion of individuals detected in the forest was higher than the actual proportion of forested area (Fig. 4; exact multinomial goodness-of-fit test, p = 0.018). Hence the dragonflies must be choosing to visit the forest habitat more often than predicted if they have no preference. Few individuals were found above water or in open environments such as grassland or path.

Discussion

Telemetry has been very useful to study habitat use and movements of insects (Kissling et al. 2014), including hornets (Milanesio et al. 2017), bees (Wikelski et al. 2010), beetles (Negro et al. 2008), crickets (Sword et al. 2008) and large dragonflies (Moskowitz and May 2017). This technique is potentially ideal to determine the habitat that each life stage of an insect preferentially selects (Moskowitz and May 2017). Here, we report that the threatened dragonfly *L. caudalis* uses the forest canopy, and very likely the top of the canopy, while they accomplish their sexual maturation phase. Other dragonfly species likely also use forests and canopies when maturing such as *Epitheca bimaculata, Somatochlora flavomaculata* and *Cordulegaster* sp. (Pajunen 1962; Corbet 1999; Ha et al. 2002; Monnerat 2013; Moskowitz and May 2017). The individuals of *L. caudalis*

were observed on the water habitat only rarely during their maturation. Our results do not exclude that these immature individuals shuttle between forest habitats and open areas such as the pond itself - indeed three detections were made in open areas and few more at the forest edge (see Fig. 1). Therefore, immature individuals are expected to feed on prey that live at the top of the canopy, including herbivorous insects, implying thereby important exchange of nutrient and energy between the aquatic and the forest habitats. This information is crucial for the conservation plans of this species: the conservation (and restoration) of the habitat of L. caudalis probably requires the conservation of deciduous forest lots composed by oaks (Quercus robur and Q. petraea) and sweet chestnut (Castanea sativa) around the aquatic habitat, but more populations/sites should be studied to confirm this association. Current conservation plans do not necessarily include forest areas around ponds, especially for populations living outside protected areas (e.g. Natura 2000 sites etc.). A large community of dragonflies and damselflies is associated with L. caudalis, and all these species should benefit from spatially expanded conservation strategies.

To the best of our knowledge, we provide the first test of telemetry on an insect ranked high in the IUCN list of threatened species (this species was 'Endangered' at the time of the study). Indeed, the application of this methodology may incur a high cost for a species which is, by definition, rather rare and/or quite sensitive to environmental stressors - including the stress of being equipped with a tag. However, this is not always acknowledged in insect telemetry studies. Among the 62 individuals equipped at the beginning of our monitoring, a small fraction was retrieved (at best 16 different individuals alive, including those that were not identified, i.e. 26%). The sampling effort (i.e., number of individuals equipped) is important to increase the chance for tracking immature individuals. This success may seem rather low compared to other studies using a similar technology. With Libellula fulva, Hardersen (2007) contacted 10 of the 16 immature individuals equipped with a similar harmonic radar. Levett and Walls (2011) equipped five Anax imperator, but only two individuals were finally tracked. Wikelski et al. (2006) detected and tracked all the 14 dragonflies (Anax junius) that were equipped. The dragonfly species cited in these studies occur in open areas, thereby maximizing detection when using an obstacle sensitive system. The behavior of L. caudalis may also partly explain why so few individuals were detected. The flight behavior of immature individuals (frequency and type) when they are at the top of the forest canopy is not documented, but frequent and rapid displacements may have limited the capability of our system to detect them-we clearly lack data on this point and our study opens new research avenues on this emblematic species.

The number of individuals that were not contacted during our study can be explained by (i) predator-induced mortality (e.g., birds), including the predator taking away the transponder or damaging it, (ii) long-range dispersal, with a fraction of the individuals flying over long distances out of reach of the telemetry system and (iii) the relatively low detection distance in the densely forested areas. Indeed, the low number of contacts after 6 days supports the two first hypotheses. The dispersal ability was shown to be up to 5-10 km (Vonwil 2005; Keller et al. 2010), but this species is considered as sedentary even by the same authors. In addition, we never detected equipped immature individuals within the 1 km radius-range outside the maturation zone defined around the pond despite extensive sampling effort with the receiver (see Fig. 3). Indeed, within our study area in 2015, L. caudalis was observed far from the detection area only rarely (2 individuals) and those were mature individuals, while many other species were found across the entire study site (Fig. S2, Table S2). A total of 27 Odonata species were observed within the study site (Table S2). Long-distance dispersal, however, would cause individuals to rapidly leave the 1 km radius range, perhaps within the first few days or even within few hours. Such dynamics is difficult to catch with the radar system. In addition, dense portions of the forest habitat prevented us from sampling equally across the study area. We estimated that the detection distance was decreased down to 20-50 m when vegetation was dense. Thus, this effect would underestimate the use of the forest habitat, thereby reinforcing our conclusions.

The predator-induced mortality has never been estimated in this species. Nevertheless, we suspect this mortality to be relatively high during the maturation phase into the forest canopy. L. caudalis is relatively small and could be a prey item for numerous insectivorous birds. Predation is often high in adults Odonata in general (Stoks and Córdoba-Aguilar 2012) and birds in particular exert a high pressure on adults (Kennedy 1950; Mitra 1977). We cannot exclude that the marking of the wings increased their visibility to bird predators, although we noticed that the contrast of the marking was low when the dragonfly was resting on plant materials. In addition, Odonata species have to acquire a large quantity of energy and nutrients during their maturation phase (Kirkton and Schultz 2001) and energy composition at emergence determine survival during the maturation phase (Stoks and Córdoba-Aguilar 2012). Females of L. caudalis increased their body mass by 160% (Table 1). The forest canopy probably offers a large amount of prey items for immature individuals to feed on, maybe at the expense of a higher exposure to predators.

Telemetry has been proven useful and somewhat efficient for analyzing the spatial distribution of insects, however, this approach still suffers from technological constraints (Kissling et al. 2014). Our prototypes of tag for the harmonic radar derived from the model created by Hardersen (2007). The final version of this tag (16.5 mg) corresponded to 10% of the weight of immature L. caudalis (including the glue and the tin used for welds). Note that mature females are heavier than males and would perform ever better with the same system. The tag used on a much larger dragonfly was about 25% of body mass (Wikelski et al. 2006), and this value was about 40% in a study on Carabus olympiae (Negro et al. 2008). Recent progress has been made allowing a tag of 12 mg only (Milanesio et al. 2016), although it is not specified whether this weight includes the glue and the welds. Not only the weight but also the dimensions of the system matter. We designed the clutter of the tag (long length) to limit its potential influence on the flight ability of the dragonfly. The tag was therefore positioned along the longitudinal plan of the abdomen. In larger species, the tag was attached to the underside of the thorax (Wikelski et al. 2006; Levett and Walls 2011), which was not possible in *L. caudalis*. The size of the tag is also constrained by the sensitivity of the emitter-receiver system. The RECCO® system allowed a descent detection distance in open areas (>100 m) and was reduced in the forest habitat. Since recently, new improved systems perform better in habitats with dense vegetation (Milanesio et al. 2016, 2017). Nevertheless, such improvements are done by researchers locally on their specific project and species, resulting in very few publications involving telemetry (no more than 3 papers per year on average; Kissling et al. 2014). A more generalized and global effort, involving industrial collaboration with researchers, is necessary to bring the telemetry of small insects several steps forward.

To conclude, the conservation biology of species using multiple habitats across their life stages, such as L. cauda*lis*, should integrate a landscape approach and the temporal dynamics of the vital domains. Several contrasted habitats can be necessary for species to complete their whole life cycle. Similar conclusions were drawn from other species; for example, females of the Hine's emerald dragonfly (Somatochlora hineana Williamson, 1931) uses dry meadows for their activities other than laying eggs, which they do in wetland habitats only (Foster and Soluk 2006). Both conservation plans and standard habitat management should consider these spatial and temporal dynamics, despite the difficulty inherent to the study of a rare and protected species. In this context, telemetry is a valuable tool to identify the various habitats used by a species. This technology remains relatively affordable but the specific application to a particular species still is time consuming due to the lack of general cohesion in the development of this methodology. But as transmitters continue to evolve and become more powerful, lighter and smaller, telemetry should allow the study of the spatial movements of insects with more precision.

Acknowledgements We thank the Tours City and the Office National des Forêts for allowing access both to the Tours-Preuilly forest and to the forest house of La Rolle. We also thank Thomas Cahon for sharing experience on the development of the tags and Emilie Deschamps for her help during the field study. This study was part of several projects: it was funded by the Foundation LISEA Biodiversité (Od'SPOT project), the Agence de l'Eau Loire-Bretagne, the Conseil Départemental d'Indre-et-Loire, the DREAL Centre-Val de Loire and the Région Centre Val de Loire (project PROTECTODO). All legal authorizations to manipulate the protected species *L. caudalis* were obtained.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Informed consent This article does not contain any studies with human participants performed by any of the authors.

Research involving animal participants All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. This research heavily involved contact with wild animals (dragonflies), and every effort was made to uphold welfare standards to reduce the likelihood of bodily harm or decreased survival because of the telemetry process. This included gentle capture, handling and release methods in suitable locations and conditions, and a method of marking the dragonflies' wings that was considered to have little effect on survival.

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