Animal Behaviour 86 (2013) 1069–1075

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Where do floaters settle? An experimental approach in odonates

Maria J. Gołąb [a,*], Szymon Śniegula [a], Szymon M. Drobniak [b], Tadeusz Zając [a], M. A. Serrano-Meneses [c]

[a] *Institute of Nature Conservation, Polish Academy of Sciences, Kraków, Poland*
[b] *Instytut Nauk o Środowisku, Uniwersytet Jagielloński, Kraków, Poland*
[c] *Laboratorio de Biología Evolutiva, Centro Tlaxcala de Biología de la Conducta, Universidad Autónoma de Tlaxcala, Tlaxcala, Mexico*

ARTICLE INFO

Article history:
Received 14 May 2013
Initial acceptance 18 July 2013
Final acceptance 20 August 2013
Available online 2 October 2013
MS. number: 13-00409

Keywords:
Calopteryx splendens
floater
habitat change
habitat quality
nonterritorial
reproductive behaviour
settlement
territoriality

According to classic ecological models, nonterritorial males should settle in low-quality habitats as a result of losing competition over reproductive sites ('defeated male' hypothesis). Alternatively, according to evolutionary game theory models, nonterritorial males should settle in the vicinity of high-quality sites and 'choose' to delay breeding until these habitats are vacant for them ('male player' hypothesis). However, nonterritorial male spatial distribution has not been experimentally tested. If the defeated male hypothesis is true (1) deterioration of high-quality sites should increase the number of nonterritorial males in a population and (2) vacated low-quality territories should be taken over by new territorial males. If the male player hypothesis is true, a similar manipulation should (1) decrease the number of nonterritorial males and (2) vacated low-quality territories should not be taken over. We performed two types of field experiment to test these hypotheses: male removal and patch quality manipulation. Our study species was the territorial damselfly *Calopteryx splendens*; males of this species exhibit both territorial and nonterritorial behaviour. Our results suggest that deterioration of high-quality habitats significantly reduced the number of nonterritorial males. The proportion of take-overs of the high-quality territories was significantly higher than that of low-quality territories. Our study supports the assumptions of the male player hypothesis and indicates that nonterritorial damselflies are more sensitive to habitat quality changes than territorial ones. Because nonterritorial individuals exist in most populations of territorial taxa, a better understanding of their settlement rules may be relevant for population dynamics and modelling.

Darwin (1876) argued that sexual selection depends on a struggle between individuals within one sex over mating success. The unsuccessful competitor leaves few or no offspring, which is equivalent to his 'evolutionary death'. Despite this, many studies on territorial species have shown that some individuals do not reproduce at a given time and do not possess territories, even though they are capable of doing so (e.g. Newton 1992). Therefore two questions arise: (1) why do nonterritorial males ('floaters') 'decide' not to reproduce; and (2) where do they settle? In our study a 'floater' is any nonterritorial male adopting a tactic alternative to territoriality (sneaking, wandering, queuing). Different studies of floaters' lifestyles have produced diverse results; however, there are two general explanations for why individuals adopt nonterritoriality. According to classic ecological models, nonterritorial males represent a reservoir of future breeders and should settle in any vacated habitats regardless of their quality (Brown 1969; Fretwell & Lucas 1969). Alternatively, floaters, using evolved decision-making rules, 'decide' to delay reproduction, even though there are vacant territories available (Kokko & Sutherland 1998) and settle in the vicinity of high-quality habitats until these become available for them. According to the latter approach, which is based on evolutionary game theory, only territories with a high expected reproductive success are occupied while territories below a given threshold quality are not (Zack & Stutchbury 1992; Kokko & Sutherland 1998).

It has been shown that bird floaters may settle in the vicinity of a given territory in order to gain knowledge about that place and conspecifics present (Smith 1978). Nonterritorial individuals could also attempt to reproduce by performing extrapair copulations (EPCs; Platek & Shackelford 2006). Intuitively, for nonterritorial individuals to succeed in obtaining EPCs, they have to appear at the breeding site for a period of time that guarantees them a mate, but it still remains unclear whether floaters choose to settle at the site or not. In contrast, other authors report that nonterritorial individuals disperse and lead a transient life at some distance from

* Correspondence: M. J. Gołąb, Polish Academy of Sciences, Institute of Nature Conservation, al. Mickiewicza 33, 31-120 Kraków, Poland.
E-mail address: marysiagolab@gmail.com (M. J. Gołąb).

0003-3472/$38.00 © 2013 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.anbehav.2013.09.013

the breeding territories (Campioni et al. 2010), ‘serving’ in a population as potential replacement individuals (e.g. Brown 1969). Finally, it has been shown that some individuals prefer to defend poor-quality territories rather than taking the risk of floating (e.g. Bayne & Hobson 2001).

In contrast to the wealth of studies focused on the consequences of habitat loss for territorial individuals, our knowledge of the reaction of nonterritorial individuals to habitat deterioration is limited (Kokko & Sutherland 1998; Penteriani et al. 2011). In their theoretical model, Kokko & Sutherland (1998) demonstrated that the loss of high-quality habitats causes not only a reduction in the reproductive population but also a greater reduction in the number of nonterritorial males. To our knowledge, experimental evidence of the settlement rules of nonterritorial males is lacking. In addition, no experiments have tested the influence of habitat quality changes on the behaviour of nonterritorial individuals.

Although widespread, territorial behaviour in insects has received less emphasis than that in vertebrates (Matthews & Matthews 2010). In territorial odonate species, nongenetically based nonterritoriality is usually classified as an inferior tactic (reviewed by Suhonen et al. 2008). However, the settlement of nonterritorial odonates has not been studied in detail. Our study organism was the riverine damselfly *Calopteryx splendens*. Sexually mature males spend their whole life at a riverside, and territorial males are attached strictly to their territories, which consist of relatively small floating vegetation clumps. Both males and females exhibit alternative reproductive tactics (Rüppell & Hilfert 1997).

With regard to the approaches presented above, we set out to test empirically two alternative hypotheses: (1) the defeated male hypothesis, which assumes that nonterritorial males should settle in low-quality patches of a habitat as a result of losing territorial contests (Brown 1969; Fretwell & Lucas 1969); and (2) the male player hypothesis, which predicts that nonterritorial males should settle in high-quality patches of a given habitat because they decide to delay breeding until these sites are available to them (Zack & Stutchbury 1992; Kokko & Sutherland 1998). The aim of this study was to test experimentally which of the two models best describes the mechanism of habitat selection in nonterritorial individuals, as well as to assess the importance of the deterioration of either high- (HQ) or low-quality (LQ) patches on the number of nonterritorial males. If the defeated male hypothesis is true, we predicted that (1) destruction (habitat patch manipulation) of the best sites should increase the number of nonterritorial males in a given area, and (2) any vacated LQ territory should be taken over. If the male player hypothesis is true (1) a similar habitat patch manipulation should decrease the number of nonterritorial males and (2) vacated LQ territory should not be taken over. We performed two types of experiment: first, male removal, to test for differences between two types of habitat (LQ and HQ) in the probability of the take-over of a vacated territory by a new territorial male and the probability of reacquisition of a territory by an original territorial male, and second, manipulation of patch quality to test for changes in the number of territorial and nonterritorial males in response to deterioration of HQ and LQ patches.

METHODS

Study Species

Calopteryx splendens is a common European damselfly, which inhabits lowland rivers (Askew 1988). The highest population density occurs in July in Central Europe (Rüppell et al. 2005; Gołąb & Śniegula 2012). The average life span of a mature male is approximately 1–2 weeks (Svensson et al. 2006; Tynkkynen et al. 2009). A male is classified as territorial when it remains close to the water surface and defends a territory (floating vegetation clumps) within 2 m of its perching site (Tynkkynen et al. 2006). Nonterritorial males usually perch on higher parts of the riparian vegetation and can exhibit both wandering and satellite tactics. Wandering males patrol large sections of a river, whereas satellite males are active along a border of one or more territories (Marden & Cobb 2004; Koskimäki et al. 2009). In our study, satellite nonterritorial males were assigned to a particular patch when they were perching up to 0.5 m from its border. Males fight with each other to gain access to a territory and also court females before copulating, and guard them during oviposition (detailed descriptions of reproductive behaviours can be found in Marden & Waage 1990; Córdoba-Aguilar & Cordero-Rivera 2005; Rüppell et al. 2005; Gołąb & Śniegula 2012).

Experimental Set-up

The study was conducted between 1 July and 5 August 2011 and 2012, on the river Biała Nida (Fig. 1), in southern Poland. It is a narrow (about 8 m wide) lowland river with a sandy bottom. The river section chosen for experiments is regulated and located in a homogeneous landscape (agricultural meadows). Hydrological conditions (water depth, velocity and temperature) of the section are homogeneous because of a weir situated 400 m downstream. The studied section was 50 m long and separated from the other parts of the river by 25 m sections that had been cleared of aquatic vegetation. Riparian vegetation was mowed regularly to prevent changes in its height (Ward & Mill 2005). All studied floating vegetation clumps (which are used by the females as oviposition patches) were cut with a pair of scissors so that the only physical factor that differentiated them was size. Every patch consisted of live *Potamogeton natans* and was situated directly adjacent to the riverbank. The patches were separated from one another by about 1.5 m. Since calopterygid females are known to prefer ovipositing on larger vegetation clumps (Waage 1987; Meek & Herman 1991), the patches were divided into two groups: HQ (large patch) and LQ (small patch). Also, based on the conspecific attraction hypothesis (e.g. Stamps 1987) and public information hypothesis (e.g. Danchin & Doligez 2001), we assumed that the presence of conspecifics reflects patch quality. Therefore, prior to manipulations, we conducted 40 min of continuous observations (see below) of every patch to assess general damselfly activity and site attractiveness to damselflies for further evaluation of patch quality (Switzer 2002a; Córdoba-Aguilar & Cordero-Rivera 2005; Guillermo-Ferreira & Del-Claro 2011). All patches were marked with a marker post (patch ID) and their areas were measured. A single patch consisted of one to four territories, depending on its size (Fig. 1).

Experiments were conducted between 1000 and 1600 hours and only under favourable and comparable weather conditions since the weather influences damselfly behaviour (Rüppell et al. 2005; Gołąb & Śniegula 2012). To avoid multiple counting, all

Figure 1. Biała Nida river. Six of the patches used in the study are visible on the right-hand side of the river.