



# Where do non-territorial *Calopteryx* males settle?

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## INTRODUCTION

Some individuals in a population do not reproduce and do not possess territories (at a given time), even though they are capable of doing so.

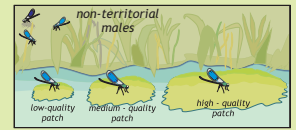
According to classic ecological models - these individuals are inferior in competition for mates and/or territories and represent a reservoir of future breeders -> **defeated male hypothesis**

Evolutionary game-theory models (Zack & Stutchbury 1992) - non-territorial males are players who use evolved decision-making rules to gain access to territories and/or mates -> **male-player hypothesis**

We performed field experiments to test these hypotheses: **male removal** and **patch manipulation**

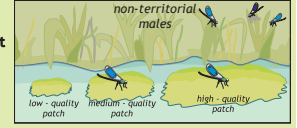
## Defeated male hypothesis

Non-territorial males settle in low-quality patches of habitat. All territories in the habitat are occupied, regardless of their quality.



## Male-player hypothesis

Non-territorial males settle in the high-quality patches of habitat and 'decide' to delay breeding until high-quality sites (HQ) are vacant for them. Only territories with a high expected reproductive success are occupied.



## male removal experiment

### METHODS

Study species - *Calopteryx splendens*. Study area - narrow lowland river Biala Nida (S Poland); July 2011 and 2012. Floating vegetation clumps were manipulated so that the size of a patch was the only factor that differentiated them (Fig 1).

We caught a territorial male and kept him for 10 min in a cool-box. In the mean time, his territory was observed until a new territorial male took it over. The time from removal of the territory owner until the taking over by a new male was noted. After the original territory owner was released, the time until reacquisition of the territory was noted.

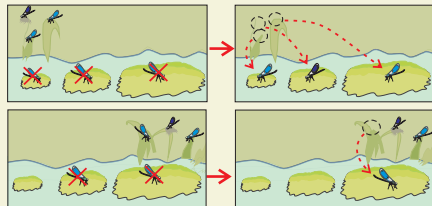
Figure 1. Biala Nida river. Six of the patches in the study area are visible on the right hand side of the river.



### predictions

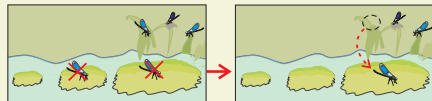
#### Defeated male hypothesis

Upon removal of territorial males, any vacated territory should be taken over, regardless of its quality.



#### Male-player hypothesis

Only vacated high-quality (HQ) territories should be taken over. Low, or medium-quality territories should stay unoccupied.



## patch manipulation experiment

### METHODS

The experiment was preceded by control observations. Each patch was observed for 20 min. Every other minute, we recorded the number of individuals displaying specific behaviors (territorial and non-territorial tactics). We counted the average number of both territorial and non-territorial males presented at each patch. After control observations, half of a given patch was sunk using ballast (Fig 2). After 5 min break another 20 min observation was conducted. Then the ballast was removed and original size of a patch was restored. The third set of 20 min observations was repeated after another 5 min break.

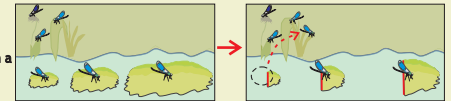


Figure 2. Patch manipulation experiment. Deterioration of patch quality with ballast.

### predictions

#### Defeated male hypothesis

Induced destruction of sites should increase the number of non-territorials in a given area



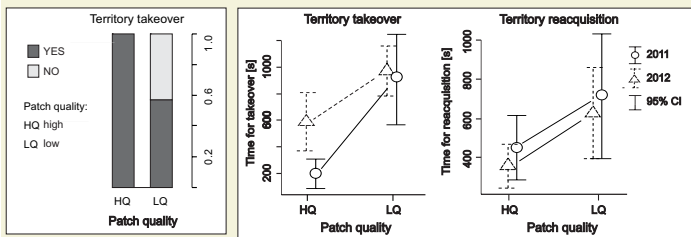
#### Male-player hypothesis

Induced destruction of sites should decrease the number of non-territorial males in a given area (Kokko & Sutherland 1998)



## male removal experiment

### RESULTS



Differences between HQ and LQ patches in the probability of territory takeover and reacquisition events

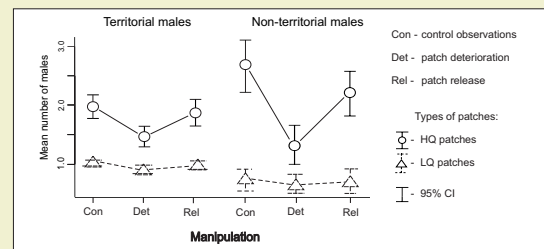
The probability of a new male taking over a vacated territory was significantly higher in HQ than in LQ patches ( $P = 0.011$ ).

Differences between HQ and LQ patches in the time new territorials needed to takeover a vacant territory and in the time original territory owners needed to reacquire of a territory

New territorial males needed less time to take over territories located in HQ patches than in LQ patches ( $P < 0.001$ ). Also the time needed for reacquisition was shorter in HQ than in LQ patches ( $P = 0.024$ ).

## patch manipulation experiment

### RESULTS



Differences between HQ and LQ patches in the number of territorial and non-territorial males in response to patch deterioration and release

The number of territorial males did not change in response to patch-manipulation ( $P = 0.237$ ) but it was different between the two types of patches ( $P < 0.001$ ). Patch-manipulation had the same effect on the number of territorial males in both HQ and LQ patches (the term *patch quality*\**manipulation* was not significant).

The number of non-territorial males changed due to our manipulations ( $P < 0.001$ ) and was different between the two types of patches ( $P < 0.001$ ). The number of non-territorials changed similarly after manipulations in both HQ and LQ patches (no interaction in *patch quality*\**manipulation* term).

Our manipulation caused higher decrease of the abundance of non-territorial males compared to territorial males.

## Read more:

Gołąb MJ, Śniegula S, Drobnick SM, Zajac T, Serrano-Meneses MA. Where do floaters settle? An experimental approach in odonates. *Submitted*  
 Kokko H, Sutherland D. 1998. Optimal floating and queuing strategies: Consequences for density dependence and habitat loss. *Am Nat* 152  
 Zack S, Stutchbury MJ. 1992. Delayed breeding in avian social systems: the role of territory quality and "floater" tactics. *Behaviour* 123

## ACKNOWLEDGEMENTS

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## CONCLUSIONS

Non-territorial males are not only unsuccessful, subordinate individuals but male-players, who can actively improve their reproductive chances.

Non-territorials settle mostly in the vicinity of high-quality sites.

Habitat disturbances affect mostly the non-territorial part of a population.