ADULT SURVIVAL OF *SYMPECMA PAEDISCA* (BRAUER) DURING HIBERNATION (ZYGOPTERA: LESTIDAE)

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The survival of hibernating adults was assessed in its winter habitat in the Netherlands to gain insight in the potential importance of this life-history phase for the population dynamics of this endangered sp. Compared to other odon., monthly survival rates (Dec. 2004 - March 2005) were high (mean $\pm$ SE = 0.75 ± 0.08), but overall winter survival was low (0.42). Potential causes of mortality during hibernation are discussed. The results imply that effective protection of this sp. in the Netherlands may benefit from protection of both its breeding and wintering habitat.

INTRODUCTION

Changes in species distribution ultimately result from changes in survival and reproductive output (STEARNS, 1992). Our understanding of why species may become more or less abundant will therefore critically depend upon insight in the key factors affecting these two major fitness components. Identification of such key factors may greatly enhance our capability of effectively protecting endangered species.

The general aim of this paper was to improve our insight in the key factors affecting the population dynamics of a rare and endangered Dutch odonate, the damselfly *Sympecma paedisca*. It is, together with *S. fusca*, the only European damselfly that spends the winter as adult (reviewed by JÖDICKE & MITAMU-

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RA, 1995; JÖDICKE, 1997). Various studies have suggested that adult survival rates in *S. paedisca* might vary substantially between years, as inferred from yearly variation in numbers of hibernating individuals (DONATH, 1981; BROCKHAUS, 1998). This life-history phase might therefore be a key in understanding the population dynamics of this species. To our knowledge, however, estimates of survival during hibernation have not yet been published. The specific aim of this paper is to fill up this gap.

In the Netherlands, *S. paedisca* has substantially decreased in both numbers and distribution since the 1960s (NEDERLANDSE VERENIGING VOOR LIBELLENSTUDIE, 2002), and is currently restricted to two populations in the northern part of the country (GRIFFIOEN & UILHOORN, 1999). Future prospects currently seem positive because the entire breeding population lies within a large protected nature reserve ('De Weerribben'). Following emergence, however, the majority of adults from these populations disperse away from the breeding habitat and hibernate outside protected areas (KETELAAR et al., 2007; MANGER & DINGEMANSE, 2007; RUITER & MANGER, 2007). Additional information on the survival prospects during hibernation will therefore provide important information on which future protection measures might be based.

METHODS

DATA COLLECTION – Data were collected on a wintering site of *S. paedisca* in the Uffelter Binnenveld, northern Netherlands, from September 2004 to April 2005. The study area consists of four ha of heath (*Calluna vulgaris*, *Erica tetralix*, *Molinia caerulea* were the dominant species) intersected by patches of pine forest (for a full description see MANGER & DINGEMANSE, 2007). During December-March (here-after called winter), hibernating adults were captured by hand, and marked with individually numbered marks on one of their wings and released at the capture location. Marks of resighted individuals were read without capture, if possible, to minimize disturbance. Capture locations were marked to enhance resighting probability of marked individuals. The study area was visited two to eight days per month and searched for about 1.5 h per day.

SURVIVAL ANALYSES – Resighting probabilities have to be accounted for when estimating survival, because some individuals escape detection while they are present and alive. We used MARK v. 3.2 to simultaneously estimate survival (ϕ) and resighting probability (p) (WHITE & BURNHAM, 1999). Sample sizes for the analysis were: 20 (number of marked individuals), 56 (effective sample size), and 44 (number of life encounters). Because ambient temperature and weather conditions can have a profound impact on survival in damselflies (e.g. THOMPSON, 1990), we expected that survival rates could vary between months. Therefore, we fitted a general model that estimated survival separately for each month. We tested the significance of month by comparing this model with a model where survival rates were equal for all months using a likelihood ratio test (LRL). Goodness of Fit (GoF) was performed on the general model using 1000 bootstrap analyses (WHITE & BURNHAM, 1999). Values of P lower than 0.05 indicate serious violations of the assumptions of the underlying model. GoF of the general model showed a non-significant lack of fit for the general model, concluding no violation of the assumptions.

RESULTS

Monthly survival rates were 0.73 ± 0.13 (mean ± SE; December-January), 0.80 ± 0.20 (January-February) and 0.69 ± 0.22 (February-March). Survival rates did not differ between months ($\chi^2 = 0.161$, df = 2, $P = 0.92$; Fig. 1a), and were on average 0.75 ± 0.08. The majority of wintering damselflies did, however, not survive the winter: we estimated that the probability to survive over the entire winter was only 0.42 (i.e. 0.75 × 0.75 × 0.75) (Fig. 1b).

Most published survival estimates are biased because (some) marked individuals fail to be resighted, not because they are dead but because they dispersed outside the study area. This study does not appear to suffer from the under-estimation of survival that would result from such a bias, because none of the resighted individuals had moved from their location of previous observation (n = 22 resightings). During this period of the year, *S. paedisca* is capable of moving using crawling or flight (see HIEMEYER et al., 2001; MILLER & MILLER, 2006). However, neither type of movement was observed during the study period. We therefore have no reason to assume that our survival estimates were biased downwards by dispersal away from the study area.

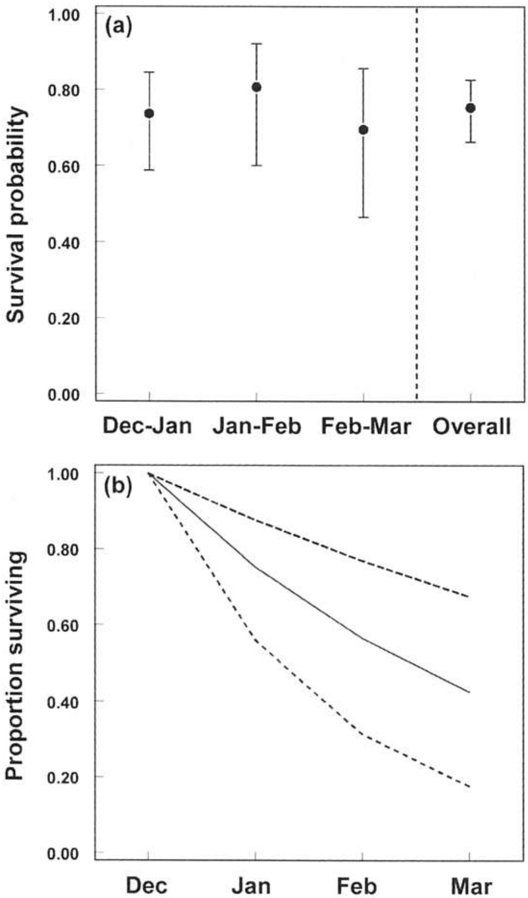

Fig. 1. (a) Montly survival rates (± SE) of hibernating *S. paedisca*; – (b) Cumulative survival rates of hibernating *S. paedisca* during winter. For each month is given the estimated proportion (± 95% confidence intervals) of individuals, marked at the onset of the study, that is still alive.

DISCUSSION

Monthly survival rates of hibernating *S. paedisca* adults were among the highest ever recorded in Odonata (reviewed by CORBET, 1999). Nevertheless, more than half of all adults that used the study area for hibernation did not survive the winter. These findings imply that the species' population dynamics is likely to be tightly linked to factors affecting survival during hibernation.

Our monthly survival estimates might have been high because published survival rates usually represent underestimates of true survival (due to permanent dispersal following marking). In contrast, dispersal did not appear to bias our survival estimates, because individuals were stationary during the period of the study. Secondly, survival rates in *S. paedisca* might be truly exceptional because its unique life-history (adult hibernation) has resulted in natural selection favouring longevity (for a discussion on the evolution of life-histories see STEARNS, 1992).

Despite the relatively high monthly survival rates, the majority of hibernating adults did not survive the winter. We have not identified which factors caused the high mortality during hibernation in our study area as deceased animals were never found. DONATH (1981) hypothesized that mortality among hibernating individuals is increased in winters with extremely low temperature. The monthly mean temperatures were, however, not extremely low when compared to other years (December 2004 through March 2005: 3.2, 5.3, 2.4, and 6.5°C, respectively; data from weather station De Bilt, central Netherlands; http://www.knmi.nl/klimatologie/maandgegevens/index.html). Therefore, low survival rates were rather linked to other environmental factors. For instance, observations from neighbouring areas used for hibernation suggest two major causes of adult mortality outside the reproductive season (RUITER & MANGER, 2007). Firstly, mass mortality due to predation by rodents. Secondly, disturbance by cattle, humans, and dogs has been observed to dislodge specimen from the plants on which they were hibernating. Increased risk of predation, and/or increased energy expenditure might thus well enhance mortality rates. Our findings therefore imply that effective protection of this species would benefit from protection of both its breeding and wintering habitat.

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