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A field study of larval development in a dragonfly assemblage in African desert ponds (Odonata)

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Abstract

Aquatic animals distributed along a 'habitat-permanence' gradient (HPG), differ in life history (Wellborn et al., 1996. Annual Revue of Ecology and Systematics 27: 337–363). Dragonflies that occur in hot arid regions often occur in temporary waters and consequently perform direct and rapid development. Dragonfly species of the Namibian desert do differ in their selection of habitats along the HPG and therefore may also differ in life cycle. Here, we attempt to monitor colonisation, larval growth and emergence in a temporary pond of known history. We studied the development of dragonfly species that laid eggs in artificial ponds constructed by us in March 2001. The assemblage consisted of species that originate from different habitats along the HPG. To obtain data on larval development we took samples from the ponds at 10-day intervals. Most species showed rapid development. By regressing the maximum sizes attained by larvae on each sampling date against time we estimated growth rates for five species and were thereby able to estimate that total duration of development from oviposition to emergence ranged between 38 and 70 days. Observation of first oviposition and first emergence for three of these species corroborated our estimates based on growth rate. Of few species, which laid eggs in the ponds no larvae or adults were found. For some this may have been the result of predation whereas others may not have grown fast enough to emerge before the ponds dried up. Our results indicate that dragonflies cannot recognise whether a pond will retain water long enough for full larval development and oviposit in waters that will not allow larval development.

Introduction

Aquatic systems can be classified with respect to the probability of drying. At one side of such a continuum are permanent waters and at the other are temporary waters (Williams, 1987; Wellborn et al., 1996; Stoks & McPeek, 2003). Whereas in permanent waters distribution of taxa is constrained by biotic factors such as predation and competition, in temporary waters it is mostly limited by physical conditions, mainly drying (Williams, 1987, 1996; Wellborn et al., 1996). One major attribute of organisms of temporary waters is rapid development; organisms of permanent waters often develop more slowly (Wellborn et al., 1996). Odonata occupy almost all kinds of habitats along the HPG ranging from permanent running waters and lakes to small temporary rain pools (Corbet, 1999). Comparative studies by Kumar (1976) in India revealed that the duration of larval

development correlates with the duration and seasonality of breeding habitats. Consequently, dragonflies show wide variation in life-cycle duration, ranging from multivoltine, having up to four or five generations per year, to partivoltine species requiring three or even more years for complete one generation (Corbet, 1999, p. 218).

In tropical and subtropical arid regions many water bodies contain water only for part of the year and Odonata species which breed in such temporary waters exhibit rapid larval growth (Hodgkin & Watson, 1958). Corbet (1999, p. 220) placed the Odonata into categories according to life-cycle features. Most widespread species of African arid regions (cf. Suhling et al., 2003) belong to type A.2.2 of Corbet (1999, p. 220). Such species are typically multivoltine and breed in ephemeral ponds during the rainy season. Nomadic adults may be carried by rain-bearing weather-fronts. A typical species of this type is the obligate circum-tropical migrant (*sensu* Corbet, 1999) *Pantala flavescens* in which the duration of larval development times can be as short as 43 days (Kumar, 1984). In other species with a similar ecology this may even be 20 days (see review in Corbet, 1999, p. 630). A further common type, A.1., is facultatively multivoltine, its aquatic habitats being continuously available. Many species may inhabit several habitat types, and may adopt a life-cycle of either type A.2.2. or A.1., depending on the type of habitat available. In both types embryonic and larval development is brief, lasting less than 120 days. A few such species are univoltine, either having an egg diapause lasting for several months or siccatating as adults (Corbet's type 2.1.2) (Suhling et al., 2003). There is no evidence to suggest that partivoltine species are to be found in desert regions (Suhling et al., 2003).

The aim of our study was to compare the larval development of some widespread African dragonfly species that occur in different habitats in the Namibian semi-desert. We assumed that all species would show rapid larval development. However, we predicted that migrants like *P. flavescens*, which regularly colonise rain-fed pools, would have higher growth rates than species that normally colonise other types of habitats. Such differences in growth rate should have consequences for reproductive success in temporary waters depending on habitat duration. We studied larval development in the field by sampling larvae from artificial ponds. To estimate growth rates from field data different methods have been used (Benke, 1970; Benke & Benke, 1975; Krishnaraj & Pritchard, 1995; Pritchard et al., 2000). In our case these methods did not yield useful data (see Methods); so we developed an alternative method. To obtain accurate data regarding duration of larval development we recorded colonisation sequence, oviposition times and emergence at our ponds.

Methods

Study area

The study was carried out at Tsaobis Leopard Nature Park (22° 22′ S, 15° 44′ E; altitude 740 m a.s.l.), 50 km S of Karibib, Namibia. Tsaobis is a private nature reserve with an area of 330 km^2 in the semi-desert/savanna transition zone (cf. Barnard, 1998) bordering the Namib-desert to the east. The climate is hot and arid most of the year. The mean monthly maximum temperatures range from 29 °C during winter (July) to 35 °C during summer (January), mean minimum temperatures being 10 and 19 °C, respectively. The temperatures at Tsaobis are usually somewhat higher (Cowlishaw & Daviers, 1997). Mean annual rainfall, which mainly occurs during the rainy season from January to the end of April, is 85 mm (Cowlishaw & Daviers, 1997; Barnard, 1998). The area is characterised by a saturation deficit of −3400 to −3800 mm per year (Barnard, 1998). All streams and springs in the park are ephemeral, but some artificial waterholes provided with ground water are permanent. Most of them are situated close to the ephemeral Swakop River, which borders Tsaobis to the north. At Tsaobis, the riverbed of the Swakop is normally dry. During the rainy season the river may run for between a few hours to some days (cf. Jacobson et al., 1995; F. Suhling, own observ.). For a detailed description of the landscape and vegetation at Tsaobis see Cowlishaw & Daviers (1997).

Artificial ponds

As part of a study on macroinvertebrate community composition of temporary ponds (cf. Padeffke