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Egg number–egg size: an important trade-off in parasite life history strategies

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ABSTRACT

Parasites produce from just a few to many eggs of variable size, but our understanding of the factors driving variation in these two life history traits at the intraspecific level is still very fragmentary. This study evaluates the importance of performing multilevel analyses on egg number and egg size, while characterising parasite life history strategies. A total of 120 ovigerous females of *Octopicola superba* (Copepoda: Octopicolidae) (one sample ($n = 30$) per season) were characterised with respect to different body dimensions (total length; genital somite length) and measures of reproductive effort (fecundity; mean egg diameter; total reproductive effort; mean egg sac length). While endoparasites are suggested to follow both an *r*- and *K*-strategy simultaneously, the evidence found in this and other studies suggests that environmental conditions force ectoparasites into one of the two alternatives. The positive and negative skewness of the distributions of fecundity and mean egg diameter, respectively, suggest that *O. superba* is mainly a *K*-strategist (i.e. produces a relatively small number of large, well provisioned eggs). Significant sample differences were recorded concomitantly for all body dimensions and measures of reproductive effort, while a generalised linear model detected a significant influence of season*parasite total length in both egg number and size. This evidence suggests adaptive phenotypic plasticity in body dimensions and size-mediated changes in egg production. Seasonal changes in partitioning of resources between egg number and size resulted in significant differences in egg sac length but not in total reproductive effort. Evidence for a trade-off between egg number and size was found while controlling for a potential confounding effect of parasite total length. However, this trade-off became apparent only at high fecundity levels, suggesting a state of physiological exhaustion.

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1. Introduction

Transition from a free-living existence to a parasitic mode of life impacted various life history traits, including fecundity (egg number) and egg size (see Poulin, 1995a; Calow, 1983). However, our theoretical framework is still lacking some important elements if we are to understand fully the mechanism of parasite egg production. These elements will allow us to evaluate the existence of general laws (i.e. patterns and processes) in parasite egg production. Furthermore, fitting the pieces of the puzzle together, namely the evidence from multilevel analyses on egg number and egg size, is crucial to elucidating parasite life history strategies.

Egg number and egg size are key concepts in parasite reproduction. For many years, our understanding of the former of these traits was largely based on the misconception that all parasites

evolve toward extremely high egg output (Poulin, 1995b). There were different explanations for it: a high egg output represents the expected outcome of natural selection – according to the ‘balanced mortality’ hypothesis (Smith, 1954), parasites must compensate for the massive losses of infective stages that occur during the transmission phase of their life cycles; a high egg output is the direct outcome of the conditions provided by the host environment (Jennings and Calow, 1975).

The strategy of egg production of a parasite is somewhere between two extremes (the *r*-end and the *K*-end) in a continuum of possibilities. It is the outcome of natural selection, representing the optimal compromise between egg number and egg size. In perfect *r*-strategist organisms, there are no density effects or competition; all available energy and matter are invested in reproduction, the smallest possible amount into each individual offspring. On the other hand, in perfect *K*-strategist organisms, the density effects are maximum and the competition is keen; the emphasis is on preserving the adult and only the remaining energy and matter are used in reproduction, i.e. in the production and maintenance of a small number of extremely fit offspring (Jennings and Calow,

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1975). The way in which parasites of a species partition reproductive effort between egg number and egg size can however vary to some extent (see e.g., Ritchie et al., 1993), i.e. reflect adaptive phenotypic plasticity. This process enables individuals to accommodate changes in their environment, by making possible the rapid movement to a new fitness optimum (Price et al., 2003); however, unlike natural selection, it does not result in genetic adaptation, i.e. in changes in genotypic frequencies in the population (Poulin, 1996, 2007).

The strategies of parasite egg production (egg number and egg size) have been addressed from broad perspectives in the literature (e.g. Gotto, 1962; Price, 1974; Jennings and Calow, 1975; Calow, 1983; Poulin, 1995a, 1996, 1997, 2007). Also, numerous studies have considered the egg production of parasites in different taxonomic groups, i.e. Monogenea, Digenea, Cestoda, Nematoda and Copepoda, in relation to different factors, i.e. adult size and longevity, maturation time or prepatency, temperature, photoperiod, salinity, season/time, sampling site, origin of the host (wild environment versus farm), host species, host size, number of parasites in the host, interactions between parasites in the host and number of treatments with anti-parasitic drugs (see e.g., Faust, 1949; Olsen, 1974; Anderson, 1982; Kennedy, 1983; Johnston and Dykeman, 1987; McGladdery and Johnston, 1988; Mehlhorn, 1988; Cable and Tinsley, 1991; Johnson and Albright, 1991; Tocque and Tinsley, 1991; Ritchie et al., 1993; Tully and Whelan, 1993; Roubal, 1994; Trouvé et al., 1998; Heuch et al., 2000; Rossin et al., 2005; Bravo et al., 2009; Bravo, 2010; González et al., 2012; Ruiz Daniels et al., 2013). Among these groups, the Copepoda is particularly suited to study parasite egg production for different reasons: firstly, copepods frequently occur in high prevalence and intensity levels year-round in their natural host populations; and secondly, unlike parasites in other taxonomic groups, copepods produce egg sacs which can be easily detached from the parasite and manipulated.

Causes of intraspecific variability in egg number and egg size can only be understood properly if the possible effects of factors at different levels, i.e. the macroenvironment, microenvironment, microhabitat (sensu Rohde, 1984) and parasite levels, are considered for analysis (see e.g. Timi et al., 2010; Loot et al., 2011). Moreover, unravelling how factors at these different levels interact with each other appears to be crucial to understanding how the mechanism of egg production works at the intraspecific level. For instance, evidence for developmental plasticity in size in response to water temperature (e.g. Nordhagen et al., 2000) and that individual parasites reach a size proportional to that of their hosts (e.g., Van Damme et al., 1993; Poulin, 1995b; Loot et al., 2011) is documented in the literature, while it is a general assumption that larger parasites tend to produce more eggs (Poulin, 2007). Larger hosts likely provide parasites with a more permanent habitat (Poulin, 2007). In this way, they may favour a delay in maturation and larger body sizes (Stearns, 1992; Roff, 1992; Poulin, 2007), therefore interfering with parasite egg production. The effect of host body size on parasite egg production appears, however, to be controversial. Actually, Cole (1954) and Kennedy (1983) argued that a decrease in parasite maturation time should result in an increase of the reproductive potential, while the same effect is expected to be seen in parasites with delayed maturity, as these should present larger body sizes. At the microhabitat level, the selective pressures affecting parasites relate to the food resources (quality and quantity) and the site of infection itself (i.e. its location within the host's body – the stress imposed on parasites living on body surfaces and in internal organs should vary greatly), as the host represents the source of food and the home simultaneously (Crompton, 1991; Castro, 1991; Combes, 1991). The nutrients available to parasites should also vary greatly with the number of conspecifics present at the site of infection, i.e. with the intensity of infection. According to the 'crowding effect' (Read, 1951), the

larger the parasite burden, the more intense the competition for essential nutrients and, likely, the host immune response; in such a scenario, both the body size and the fecundity of the parasite are expected to be negatively affected. This type of effect has been documented for cestodes (Keymer et al., 1983; Dobson, 1986; Shostak and Dick, 1987; Heins et al., 2002), nematodes (Krupp, 1961; Khamboonruang, 1971; Michel et al., 1971, 1978; Szalai and Dick, 1989) and digeneans (Jones et al., 1989).

A phenotypic trade-off between egg number and egg size has already been demonstrated using data from different taxa of parasitic copepods (see Poulin, 1995a, 2007), but its occurrence at the intraspecific level is less consensual (see e.g., Rossin et al., 2005; Timi et al., 2005). The trade-off appears to be influenced by a number of factors, i.e. the host quality (Rossin et al., 2005), the female body size (Herrerias et al., 2007) and the site of infection (Loot et al., 2011), which should therefore be considered for analysis.

This study aimed to investigate how the mechanism of egg production works in parasites using a multilevel approach. Particular emphasis is given to the trade-off between egg number and egg size and the factors having a significant influence on these two life history traits. *Octopicola superba* (Copepoda: Octopicolidae), parasitic on the common octopus, *Octopus vulgaris* (recently suggested to represent a complex of species), was used as a model parasite. Data were assessed from mature, ovigerous females. The specific questions addressed were the following: (i) which strategy of egg production is followed by the parasite: is it mainly an *r*-strategist (i.e. produces a large number of small, poorly provisioned eggs) or a *K*-strategist (i.e. produces a small number of large, well provisioned eggs) species; (ii) was there an influence of season, site of infection, host body size, number of conspecifics present at the site of infection and parasite body size (or of interactions between these variables) in egg number and/or egg size; and (iii) was there a phenotypic trade-off between egg number and egg size, while controlling for a potential effect of confounding variables? While considering each of these questions, the existence of general trends was evaluated on the basis of the information available in the literature.

2. Materials and methods

2.1. The parasite

Octopicola superba is a parasite of *O. vulgaris*, endemic to European waters (Humes, 1957; Deboutteville et al., 1957; Bocquet and Stock, 1960; Cavaleiro et al., 2013). It most likely has a single host life cycle. Indeed, according to our findings, both copepodites and adults are commonly found on *O. vulgaris*. Information on this parasite is scarce concerning its behaviour (Deboutteville et al., 1957) and infection levels (Bocquet and Stock, 1960). Associated disease is not documented in the literature, which suggests that *O. superba* might not be pathogenic for the natural population of octopus; otherwise, the lack of records on associated disease is likely a consequence of the low number of studies so far conducted on this parasitic infection. According to our findings, ovigerous females of *O. superba* are present at high prevalence and intensity and year-round on *O. vulgaris* off northwestern Portugal. The parasite can be easily isolated from the sediment obtained from the washings of the octopus' body surface and mantle cavity. All of these aspects make it ideally suited to study the mechanism of egg production in parasites. Besides, species associated with marine invertebrates seem to be particularly suited to studies of the impact of the type, habitat and behaviour of the host in the number and size of the eggs laid by the copepod (see Gotto, 1962).

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