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Reproductive anatomy and fecundity estimation of the haematophagous ectoparasite *Carnus hemapterus*

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Abstract The dynamics of host–parasite interactions depends to a large extent on the effect of host responses on parasite fitness. An increased research effort is currently being invested in the study of host influence on parasite fitness both at a population and at an individual level even though basic information (e.g. the reproductive anatomy of parasites) is frequently missing. Here, we study for the first time the reproductive system of the diptera *Carnus hemapterus*, a 2-mm long, highly mobile haematophagous fly parasitizing nestlings of a broad variety of bird species. Although this species is poorly known, it is being increasingly used for the study of host–parasite interactions. We also assess the reliability of a method to estimate fecundity based on the number of laid eggs per gravid female and analyse the effect of body size on fecundity estimates. Our results show that carnid flies are synovigenic, so that both the number of laid eggs at a given moment and the egg load represent only a fraction of the true potential fecundity. Moreover, laid eggs are probably a fraction of the number of mature eggs ready to be laid since females withheld seemingly mature eggs at oviposition. A high proportion of pregnant females did not lay eggs, and the number of eggs laid per pregnant female varied remarkably. The latter is explained partly by a positive relationship with body size (thorax length and abdomen width). Caution is needed when using the number of laid eggs as a shortcut estimation of fecundity in *C. hemapterus*. We propose some improvements to the method for assessing *Carnus* fertility.

Introduction

Understanding the dynamics and evolution of host–parasite interactions requires knowledge about fitness achieved by both protagonists (Walker et al. 2003). Whereas the impact of ectoparasites on their hosts has been studied for many systems (see Møller et al. 1990; Fitze et al. 2004 and references there in), the effects that host characteristics and responses have on parasite fitness parameters have been neglected till recently (Krasnov et al. 2005). The study of factors affecting the reproductive success of parasites could be particularly fruitful since the reproductive success of parasites is likely to depend more strongly on host characteristics than parasite intensity (Heeb et al. 1996; Roulin et al. 2001). Fecundity of parasites has also been used as a measure of host susceptibility to parasites (see Roulin et al. 2007). However, detailed data on the factors affecting fecundity of ectoparasites are frequently missing. Several reasons may account for this. First, studying the effect of the parasite on host fitness, rather than the opposite, is usually of greater relevance for human and animal welfare. Second, fecundity is difficult to estimate and poses both conceptual and methodological problems. Fecundity, a term that refers to the reproductive potential of an individual, can be expressed in different ways (Mills and Kuhlmann 2000): maximum fecundity, potential fecundity

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and realized fecundity. Whereas estimations of potential and realized fecundity of insects can be obtained from more easily measured parameters (e.g. egg load, number of ovarioles), several authors have warned that such shortcuts cannot be accurate enough and that several variables can confound the adequacy of such estimates (Leather 1988; Mills and Kuhlmann 2000). Finally, both flawed methodological approaches to the study of fecundity and overlooking of key factors affecting egg production (e.g. body size, age, life cycle) may lead to biased results.

During the last years, the increased interest of evolutionary biologists and ecologists on host–parasite relationships has fuelled the study of host influence on parasite fitness. Several authors initiated the study of parasites' reproductive success at a population level (i.e., estimating the number of descendants per a known number of adults) without considering intraspecific variability (see, for instance, Lee and Clayton 1995; Heeb et al. 1996; Tripet and Richner 1999a, b; Møller 2000). Recently, several studies have focused on the effect of host characteristics on parasite fitness at an intraspecific level (Walker et al. 2003; Krasnov et al. 2005; Roulin et al. 2001, 2007; Tschirren et al. 2007). However, lack of basic information (e.g. reproductive anatomy and physiology and the factors influencing reproduction in insects) may limit our progress in such studies by restricting the number of biological systems to be studied and by overlooking key factors critically influencing fecundity, like longevity or size (Leather 1988).

Carnus hemapterus, a 2-mm long, highly mobile haematophagous fly parasitizing nestlings of a broad variety of bird species (Grimaldi 1997), was ignored for a long time except for entomologists and parasitologists (e.g. Bequaert 1942; Lloyd and Philip 1966). Its potential detrimental effect on nestling health became an interesting issue (Whitworth 1976; Cannings 1986) whose study stimulated ecological studies on the species (Kirkpatrick and Colvin 1989; Dawson and Bortolotti 1997; Liker et al. 2001). More recently, it is being increasingly used as an appropriate system for studying the evolution of host–parasite interactions (Soler et al. 1999; Valera et al. 2004; Václav et al. 2008; Chakarov et al. 2008; Hoi et al. 2010), including parasite fitness (Roulin et al. 2001, 2003). Yet, our knowledge about aspects like life cycle, morphological and physiological parameters of reproduction as well as about the validity of methods used to estimate fecundity (Roulin 1998; Roulin et al. 2001, 2007) is scarce, what hinder further progress.

The aims of our study are: (1) to provide basic information on the reproductive anatomy and fecundity of *C. hemapterus*, (2) to assess the validity of an experimental method to estimate fecundity in this species, (3) to explore whether the general relationship between body size and fecundity (Fox and Czesak 2000; Branquart and Hemptinne 2000; Rossin et al. 2005) is applicable in *C. hemapterus.*

Materials and methods

Study area and study species

The study area was located at the Desert of Tabernas (Almería, southeast Spain, 37°05′N, 2°21′W). Climate in this area is semi-arid with long, hot summers and high annual and seasonal variability of rainfall (mean annual rainfall, 218 mm).

The life cycle of *C. hemapterus* comprises an adult stage, three larval phases encompassing around 21 days at 22°C and 95% relative humidity and a nymphal stage. After a diapause usually lasting several months (Guiguen et al. 1983; but see Valera et al. 2006), nymphs emerge the following spring at the time after nesting sites have been reoccupied by birds. Adults are initially winged and capable of flying, but they typically lose their wings once they have found a suitable host (Roulin 1998, 1999). Copulations take place on the host (Guiguen et al. 1983). Gravid females are easily recognizable by the white, enlarged abdomen. Key aspects of the reproductive physiology, life cycle and behaviour of this parasite, like oogenesis, longevity or feeding rate are, to our knowledge, unknown.

The European roller *Coracias garrulus* (hereafter just roller) is a common avian breeder in the study area, occupying natural holes excavated in sandy cliffs as well as cavities in human constructions and nest boxes. *C. hemapterus* infestation in our study area is high, with 100% prevalence and a load ranging from a few flies to several hundreds per nest (Václav et al. 2008).

Estimating fecundity

To our knowledge, a single method for estimation of *C. hemapterus* fecundity has been reported (Roulin 1998; Roulin et al. 2001, 2007). It estimates fecundity on the basis of number of laid eggs per gravid female kept under artificial conditions.

During the period 19–28 June 2007, 39 gravid *C. hemapterus* females were collected from unfeathered roller nestlings in nine nests. Following Roulin (1998) and Roulin et al. (2001, 2007), each female was put separately in a tube (in our case a glass tube closed with cork). Living females in tubes were stored at 37°C. As reported by Roulin et al. (2001, 2007) after 24 h, all flies were dead. When egg laying occurred, the number of laid eggs in the tubes was counted.

Whereas this method seems an easy, viable approach given the difficulties posed by the study species (e.g. highly mobile, small individuals feeding on nestling birds of wild species), no attempt to assess its validity has been done to our knowledge.

Reproductive anatomy of the parasite

To gain knowledge about the reproductive anatomy of *Carnus* and to assess the reliability of fecundity estimates obtained by the above-mentioned method, dead females were collected from the glass tubes and were kept at 4°C until they were dissected. The abdomen of each specimen was opened, and the ovaries with eggs were taken out carefully under the stereo-microscope. The eggs were gently separated out into physiological solution. Microscopic slides with eggs were transferred to a microscope where several morphs could be distinguished: large, striated, chorionated mature eggs; medium-sized, brownish eggs; and whitish, highly immature, small eggs (see "Results"). The number of chorionated and brownish eggs were counted under the microscope using a striped microscopic slide. Small eggs were not counted since not all could be individually differentiated (Fig. 1). Eggs were counted with an × 40 augmentation. For a subset of flies, the number of chorionated and brownish eggs were counted three times and repeatability calculated following Lessells and Boag (1987). Repeatability of counts of both types of eggs was high (r_i=0.997, $F_{9,20}$=1,322.4, p<0.001; r_i= 0.988, $F_{9,20}$=173.5, p<0.001, respectively).

Body size and fecundity

As estimators of body size, length, and maximum width of abdomen and thorax of each female was measured prior to dissection with a stereo-microscope (Zeiss, ref. 475052–9901) fitted with an ocular micrometer (1 ocular unit=0.02 mm, all measured at × 50 magnification) (Norry et al. 1999; Smith and Lamb 2004).

Fig. 1 Detail of the morphology of the reproductive system of female *C. hemapterus*. Several ovarioles with follicles at different degree of maturity can be seen. The least mature follicles are formed at the distal part of the ovariole (germarium). Follicles become mature (i.e. larger) as we move away from the germarium, so that mature, chorionated follicles can be observed at the lower part of the picture

Statistical analyses

Regression analyses were used to highlight the relationships between laying, number of mature and immature eggs, and body size. In a first analysis, our dependent variable had a binary nature: "laying females" versus "non-laying females". A logistic regression was used with predictor variables being number of brownish eggs, number of chorionated eggs, and thorax and abdomen length and width. Additionally, to examine whether body size and/or the amount of maturing eggs explained clutch size a standard multiple regression was used. The dependent variable was the number of laid eggs, and the independent variables were thorax and abdomen length and width and the number of both egg types in the abdomen. Parametric tests were used where the assumptions for normality were met. Unless otherwise stated, tests are two-tailed and means ±1 SE are presented throughout the article.

Results

Reproductive system of *C. hemapterus*

Dissections evidenced the occurrence of eight ovarioles where the follicles (i.e. developing eggs) are formed and mature (Fig. 1). A succession of follicle maturity is established along the ovariole, with the youngest, least mature follicles located in the distal portion of the ovariole and the more mature follicles found closer to the oviduct. Three morphs could be easily distinguished: small, transparent follicles; medium-sized, brownish follicles; and large, striated, chorionated eggs, with similar size to the ones laid (Fig. 2). To test whether laying females were withholding eggs at oviposition, we dissected females after they had laid. In all cases, we found mature (chorionated) eggs. We also found mature eggs in non-laying, dead females.

Laid eggs as an estimator of fecundity

Twenty-two (56.4%) out of 39 flies laid at least one egg. The mean number of laid eggs was 38.7±3.9, and it ranged from 11 to 81 (C.V.=47.6%) (Fig. 3).

After laying, females still kept eggs in the abdomen (Fig. 1). Small, whitish, recently formed follicles were present in all females. Brownish, medium-sized eggs averaged 41.8±3.1 per laying female (range, 15–71).

Fig. 2 *C. hemapterus* eggs. Mature, chorionated, unlaid egg (**a**) and laid egg (**b**)

Chorionated eggs, averaging 34.4±3.6 per laying female (range, 6–64) were similar in size to laid eggs (Fig. 2).

The number of laid eggs was not correlated either with the number of chorionated eggs (Spearman correlation, r=0.04, p>0.10, n=22), the number of brownish eggs (r=0.25, p>0.10, n=22) or the sum of both types of eggs (r=0.15, p>0.10, n=22).

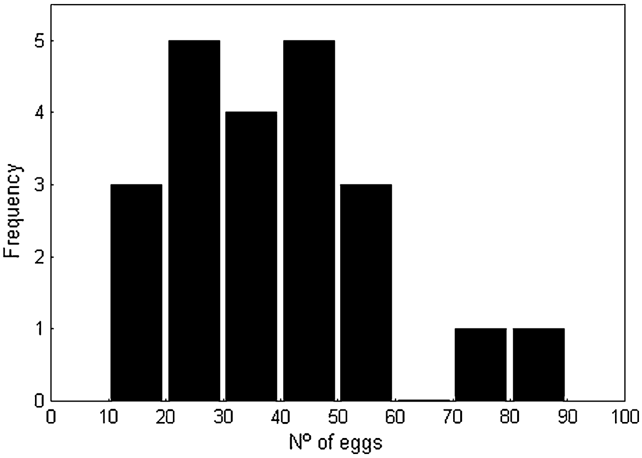

Fig. 3 Frequency of clutch sizes of 22 *C. hemapterus* females having laid at least one egg

Females that did not lay any egg had chorionated (mean±SE, 35.6±3.6; range, 5–61; n=17), brownish (mean±SE, 38.1±2.8; range, 15–55; n=17) and whitish, highly immature eggs in the abdomen.

The number of chorionated and brownish eggs did not differ between laying and non-laying females (t tests: t=0.22, p>0.10, df=37; t=0.85, p>0.10, df=37, respectively).

Determinants of laying and clutch size

We obtained no significant model when trying to explain laying vs. non-laying on the basis of thorax and abdomen dimensions and number of brownish and chorionated eggs (logistic regression, χ^2=4.56, df=6, p=0.60).

Concerning variation in the number of laid eggs, a multiple regression analysis with body size and number of brownish and chorionated eggs as independent variables provided a significant model ($F_{6,15}$=3.28, p=0.028, R^2=0.57) in which thorax length and abdomen width were positively correlated to number of laid eggs (β=0.61, p=0.02; β=0.49, p=0.054). In contrast, abdomen length was negatively related to the amount of laid eggs (β=−0.53, p=0.026).

Discussion

This study provides for the first time basic information on the reproductive anatomy and fecundity of the haematophagous ectoparasite *C. hemapterus,* that it is useful for a better understanding of the reproductive physiology of this parasite and to evaluate the reliability of estimators of fecundity. Since we collected gravid females, we are unable to report on egg maturation at the time of emergence (and thus on significant fitness variables like the ovigeny index and initial egg load, see Jervis and Ferns 2004). However, we did record continuous maturation of follicles and since flies of different ages were probably sampled (adult *C. hemapterus* emergence is continuous, Valera et al. 2003, 2006) our results suggest that carnid females are synovigenic. This is important because it implies that both the number of laid eggs at a given moment and the egg load (the number of mature eggs carried by a female at a given moment in her lifetime) represent only a fraction of the true potential fecundity.

Concerning fecundity estimates, our results are similar to those obtained by Roulin (1998): (1) 44% of females did not lay eggs, similar to the 42% found by Roulin (1998); (2) the mean number of laid eggs in this study (38.72±

SD 18.43) is close to the one reported by this author (45± SD 18) even though he found a broader range of laid eggs (up to 109) than we (maximum number of laid eggs=81).

We could not explain the occurrence of egg laying on the basis of body size and number of eggs in the abdomen. Since non-laying females had similar number of mature and maturing eggs in the abdomen to females that laid eggs we suspect that some of them (those with a large number of chorionated eggs) could have retained the eggs waiting for a suitable oviposition substrate whereas others (those with a small number of chorionated eggs) were probably not prepared to lay eggs at the moment because they could have already laid a previous clutch short before.

Concerning clutch size variation in laying females we found that the number of laid eggs was partly explained by body size (females with larger thorax and wider abdomen laid more eggs), as expected from the generally accepted relationship between body size and fecundity (Fox and Czesak 2000; Branquart and Hemptinne 2000; Rossin et al. 2005). However, we also found a negative relationship between abdomen length and number of laid eggs. This could simply indicate a shortening of the abdomen after laying. An alternative explanation is that females accumulated eggs at the end of the abdomen. It is known for several species that in the absence of oviposition sites, females refrain from ovipositing. Eggs can then be reabsorbed (e.g. Branquart and Hemptinne 2000) or accumulated in the abdomen, especially if the insects are held in containers that do not have suitable substrate in which to lay their eggs. In this case, eggs are ovulated (i.e. passed from the ovariole into the lateral oviduct) but held in the oviducts until suitable oviposition substrate is found (e.g. Tammaru and Javois 2000; Mefferd et al. 2005; Takahashi 2007). Thus, it could also be that the number of laid eggs is a function of the storage capacity of the females.

To what extent is this method reliable to estimate fecundity of *Carnus*? Our results suggest that caution is needed when using the number of laid eggs as a shortcut estimation of fecundity in this species. The occurrence of a large number of flies laying clutches above the average (see Figs. 1 and 2 in Roulin 1998) together with our findings that females that laid eggs still held chorionated (mature or almost mature) eggs in the abdomen suggest that many females withheld mature eggs at oviposition. Therefore, laid eggs are probably a fraction of the number of mature eggs ready to be laid (egg load). The lack of correlation between the number of laid eggs and non-laid eggs precludes any inference about how well the former represents egg load. Moreover, egg load is probably only a fraction of the true potential fecundity (see above). An accurate estimation of fecundity in *C. hemapterus* would require information about the adult lifespan, which strongly determines the net reproductive rate (Holmes and Birley 1987). Moreover, since in haematophagous diptera ovulation and oviposition usually depends on previous blood feeding, the biting frequency will also determine the life fecundity (Holmes and Birley 1987; Briegel and Horler 1993; Hogg et al. 1997; Kassem and Hassan 2003). In absence of such information, egg load is probably a more accurate shortcut fecundity estimator than the number of laid eggs. Using the later parameter to study intraspecific variation in fecundity would require some cautionary measurements (see, for instance, Agnew and Singer 2000; Krasnov et al. 2005; Tschirren et al. 2007). Concerning *Carnus*, whereas it makes sense to discard those flies that did not lay eggs (see Roulin et al. 2001, 2007), considering flies that laid abnormally low number of eggs probably produces some bias since such low fecundity is very likely fictitious.

Improvements to the method here tested should attempt to control the main factors that influence the reproduction of the species: microclimate, age, oviposition conditions, egg maturation strategy, etc. (see, for instance, Krebs and Loeschcke 1994; Lourenco and Palmeirim 2008; Adham et al. 2009). Whereas some factors can be difficult to manipulate, others could possibly be improved. Several hints suggest that rearing conditions were probably stressful for gravid females. More than 40% of flies did not lay eggs (even though dissection showed that non-laying females were actually parous ones since they held mature eggs in the abdomen, range, 5–61) and all flies died after 24 h. In the absence of information about the optimal temperature for carnid flies, 37°C seems to be high for other dipterans (Schnebel and Grossfield 1986; Kimura 2004). Moreover, although flies probably spend much time on the hosts, they also move around and are frequently found on the nest material (where temperature usually drops below 30°C, see, for instance, Rahn et al. 1983; Dawson et al. 2005). In fact, we have frequently observed females laying on the nest debris, under the nestlings (personal observation). Humidity should also be considered. Humidity is usually high in nests of troglodyte birds (common hosts of *C. hemapterus*), where it can reach 100% (Lill and Fell 2007). Thus, the interaction of heat and desiccation (tubes were not moistened) can account for the death of many females, in some cases probably before they could lay, and could even influence the reproductive output of laying females (see Krebs and Loeschcke 1994).

Words of warning when estimating total fecundity using shortcut fecundity estimates have been stressed since long (Leather 1983, 1988; Mills and Kuhlmann 2000). The reliability of different shortcut fecundity estimates in insects will vary according to the characteristics of the particular study system but will surely depend on whether we control for the main factors that influence their reproduction. Being

Carnus a haematophagous insect, we think that information about its autogenous or anautogenous nature and the relationship between feeding frequency and laying is basic (see, for instance, Sutcliffe et al. 1993; Briegel et al. 2002; Kassem and Hassan 2003; Jervis and Ferns 2004). In the absence of such information, cautionary measurements like collecting gravid females prior to laying (those placed on the nest debris, under the nestlings) and improvements (e.g. placing flies in porous tubes with some debris into and keeping them in the nest or unoccupied cavities while females lay) will probably help to standardize influencing factors. Dissection of a subsample of flies will serve to check for egg retention.

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