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Old pythons stay fit; effects of haematozoan infections on life history traits of a large tropical predator

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Abstract We document the impact of blood parasite infections caused by *Hepatozoon* sp. on water python (*Liasis fuscus*) life history traits such as growth rates, condition, reproductive output and survival. Individual snakes maintained similar among-year parasite loads. *Hepatozoon* infections affected python growth rate, i.e. snakes suffering from high infection levels exhibited significantly slower growth compared to individuals with low parasite loads. Our results suggest that the parasites also affected the pythons' nutritional status (condition), as snakes with low condition scores suffered from higher parasite infection levels than snakes with high scores. Furthermore, our data suggest that parasitaemia may affect female reproductive output, as reproductive female pythons harboured lower parasite loads compared to non-reproductive adult females. High levels of parasite infections also affected juvenile python survival, as recaptured snakes harboured significantly lower parasite loads compared to non-recaptured yearling pythons. In our study area, water python have very few natural predators and, hence, experience low mortality rates and commonly reach an age of >15 years. In contrast to results obtained in other studies, parasite loads in larger/older pythons were lower compared to younger snakes, suggesting that only snakes harbouring lower levels of parasitaemia were able to survive to old age. We suggest that a possible cause for the opposing results regarding parasite prevalence and host age may be due to different levels of extrinsic mortality rates and longevity. Long-lived organisms, such as water pythons, may invest relatively more into crucial self-maintenance functions such as parasite defence, compared to short-lived organisms.

Keywords Blood parasites · *Hepatozoon* · Snake · Life history · Australia

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Introduction

A feature of many host–parasite associations is that most of the hosts within a population tend to harbour few parasites whereas only comparatively small numbers are heavily infected (Moritz et al. 1991; Poulin 1993). Infections by some parasites, such as protozoans, are extremely prevalent and haematozoans have been observed in all vertebrate host species so far examined (e.g. Telford 1984; Appleby et al. 1999). This group of parasites infect and multiply in host erythrocytes but their effects on host fitness have been debated. Many studies have detected no or only marginal effects of haematozoan infections in divergent vertebrate taxa such as lizards, snakes and birds (Wozniak et al. 1994; Weatherhead 1990; Dale et al. 1996; Eisen 2001), whereas other studies have demonstrated severe pathological effects, e.g. leukocytosis, anorexia, myopathy and even death (Atkinson and van Riper 1991; Wozniak et al. 1996; Oppliger and Clobert 1997; Merino et al. 2000). In order to understand evolutionary interactions occurring between haematozoan parasites and their hosts, we need to know the extent to which parasites may cause detrimental effects on host life history traits, such as growth, condition, reproductive success and survival.

Since 1987 we have been conducting field work on a large population of water pythons (*Liasis fuscus*) on the Adelaide River floodplain, situated 60 km south east of Darwin in the Northern Territory of Australia. During the course of the study, we came to realize that the pythons were frequently infected by blood parasites, that in some cases appeared to have resulted in death of the

snakes (T. Madsen et al., personal observation). Consequently, in recent years our work has focused on quantifying individual variation in haematozoan parasite prevalence and documenting their possible effect on python fitness.

In snakes, members of *Hepatozoidae* have been reported to be the most prevalent group of intracellular blood parasites (Telford 1984; Wozniak et al. 1996). In a previous study we confirmed that the infections observed in water python erythrocytes were indeed caused by *Hepatozoon* sp. (Ujvari et al. 2004). This group of protozoans has a heteroxenous life cycle involving merogony and gamogony within the vertebrate host and sporogony within an invertebrate vector (Telford 1984). Anopheline and culicine mosquitoes, ixodid ticks and phlebotomine sand flies have all been shown to be experimental vectors (Telford 1984). Several studies have suggested that these haemogregarines appear to be well tolerated by their natural hosts (Nadler and Miller 1984, 1985; Wozniak et al. 1994). However, preliminary data from our 17 years of study of water pythons suggest that *Hepatozoon* infections may indeed affect several fitness-related traits. In the present study we therefore explore how *Hepatozoon* loads may affect python life history traits such as growth rate, condition, reproductive output and survival.

Materials and methods

Study area and species

The study was conducted in the Fogg Dam conservation reserve, in the lower reaches of the Adelaide River floodplain 60 km south east of Darwin in the Northern Territory of Australia. The area lies within the wet–dry tropics. Temperatures are high year round (mean daily maximum air temperature $>30°C$ in every month) but precipitation is concentrated in a brief (3 month) wet season; rainfall is highly variable among years. The Adelaide River floodplain is a relatively flat, treeless area formed by silt deposition from the river that is inundated by monsoon rains each year (for a more detailed description of the study area, see Madsen and Shine 1996a).

Water pythons (*L. fuscus*) are large (up to 3 m) non-venomous snakes widely distributed across tropical Australia (Cogger 1992). The results in the present paper are primarily based on a capture–mark–recapture study of pythons collected in the Fogg Dam conservation reserve between 2001 and 2003. The snakes were captured at night by spotlighting (on foot, or from a slowly moving vehicle), and released the following day after they had been measured, weighed, sexed, and individually marked for later recognition (see Madsen and Shine 1996a, b for further details). In our study area reproduction is highly seasonal, most of the matings occur in July to early August and oviposition from September to mid October. During this period we can confidently distinguish reproductive from non-reproductive females (Madsen and Shine 1996b).

In order to explore the effects of parasitaemia on python nutritional status, we calculated an index of body condition for each snake (using residual scores from the general linear regression of ln-transformed mass to body length). Thus, high condition scores reflect relatively larger amounts of stored fat bodies (Weatherhead and Brown 1996; Bonnet et al. 1998).

Detection of parasites

Blood parasites were examined by placing a drop of blood, obtained by cutting off approximately 2 mm of the snakes' tail tips, directly onto a glass slide and smearing it with a second slide to produce a one-cell-thick blood layer. The blood smears were air dried, fixed in methanol and stained with Giemsa. Each slide was examined under oil immersion (×100). A total of 2,000 red blood cells were analysed per slide and infection intensity quantified as number of infected erythrocytes. Blood smears from 329 pythons were examined (149 in 2001 and 180 in 2002). In addition 36 pythons sampled in 2001 were recaptured in 2002 and their parasite loads were re-sampled. Thirty-two pythons were recaptured in 2003 of which five were examined in 2001 (not included among the 36 pythons recaptured in 2002) and 27 first examined in 2002. Unfortunately, the samples collected in 2003 were lost in transport between Sweden and Australia and could therefore not be included in our analyses. To determine whether a single blood sample provided reliable data on parasite load, 15 pythons were sampled twice within a month. The two parasite counts revealed a highly significant correlation ($r=0.99$, $P=0.0001$, $df=14$) strongly suggesting that the infection level recorded when performing only a single count yields a robust measure of *Hepatozoon* infection levels.

Statistical analysis

As distribution of parasite infection level was highly skewed; this variable was $\ln(x+1)$ transformed and examined for normality using Shapiro-Wilkes' statistics before being submitted for statistical analysis.

Results

Among-year variation in haematozoan infection level was determined from the 36 pythons initially captured in 2001 and subsequently recaptured in 2002. Regression analysis revealed a significant among-year relationship, i.e. pythons with high parasite infection levels in 2001 were also suffering from heavy parasite loads in 2002 ($r=0.84$, $P=0.0001$, $df=35$, Fig. 1).

Python growth rate is size/age specific (Madsen and Shine 2000). Thus, in order to eliminate the effect of

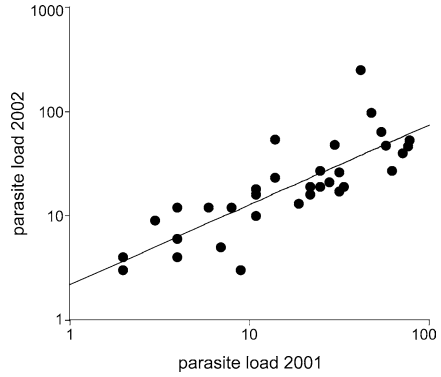

Fig. 1 Relationship between python parasite loads in 2001 and 2002

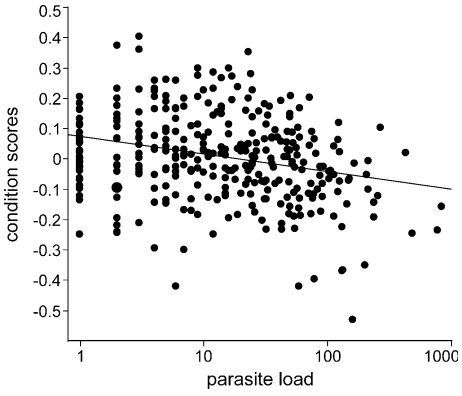

Fig. 3 Python condition scores (residuals from a mass-length regression of ln-transformed data) in relation to parasite load

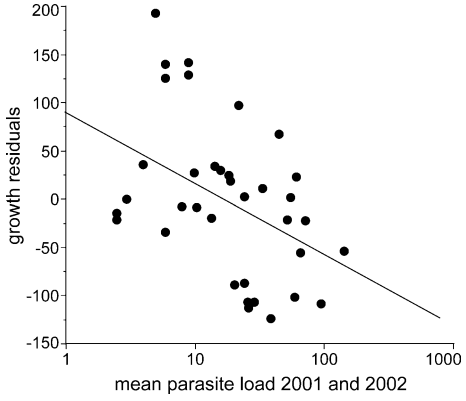

Fig. 2 Python growth residuals in relation to mean parasite load. Growth based on residual scores from a linear regression of daily growth increment and body length

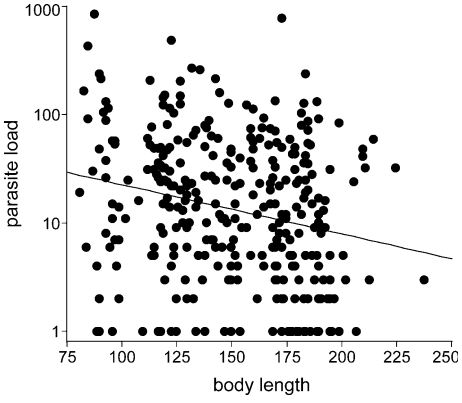

Fig. 4 Relationship between parasite load and python body length

body size on growth, growth was based on residual scores from a linear regression of daily growth increment on size. Although the pythons maintained a similar among-year level of parasite infections, temporal differences were detected (Fig. 1). We therefore used the mean value of the number of parasites per snake in 2001 and 2002, to investigate whether parasite infection level affected python growth rate (the data were subsequently ln-transformed). The analysis revealed a significant negative relationship between python growth rate and parasite infection level ($r = 0.47$, $P = 0.005$, $df = 35$, Fig. 2).

We did not detect any difference in parasite infection level due to sex among the 182 male and 147 female pythons sampled ($t = 1.19$, $P = 0.23$, $df = 327$). However, our results suggest that haematozoan infection level affected python nutritional status, i.e. pythons with a higher condition score harboured lower parasite loads compared to snakes with lower scores ($r = 0.24$, $P = 0.0001$, $df = 328$, Fig. 3). Furthermore, our results also suggest that haematozoans affected female python reproductive status. When comparing the parasite loads of reproductive and non-reproductive adult female pythons captured in August and September 2001 and 2002, we detected a significant difference between the two female categories, with reproductive females harbouring significantly lower haematozoan loads compared to non-reproductive adult female pythons ($t = 2.85$, $P = 0.006$, $df = 61$).

Although the water pythons at our study site show considerable among-individual variation in annual growth rates, python body size is still a robust predictor of python age, i.e. large snakes being older than smaller individuals (Madsen and Shine 2000). Examination of the relationship between size/age and parasite infection levels disclosed a significant negative relationship, that is, larger/older snakes had lower parasite loads compared to smaller/younger snakes ($r = 0.23$, $P = 0.0001$, $df = 328$, Fig. 4).

Using logistic regression, and recaptured versus non-recaptured scores as an index of python survival, we compared the parasite load among these two categories. The overall recapture records of the 149 snakes initially captured in 2001 and the 180 initially captured in 2002 revealed no difference in parasite loads (Walds' $\chi^2 = 1.09$, $P = 0.30$, $df = 1$), whereas body length had a significant effect on recapture probability (Walds' $\chi^2 = 15.13$, $P = 0.0001$, $df = 1$). However, immune function in several taxa, including reptiles, has been

documented to be depressed in juveniles compared to adults (Grindstaff et al. 2003). Furthermore, in great tits (*Parus major*) Hõrak et al. (2001) demonstrated that non-infected yearlings survived better than infected ones, whereas survival in older birds revealed an opposite result. Thus, selection can be expected to operate much more strongly on yearlings than older snakes, which warrants a separate analysis of this cohort. We therefore continued our analysis with a separate logistic regression on yearling pythons (body size of 80–110 cm; Madsen and Shine 2000). This analysis suggests that haematozoan infections levels indeed affected the recapture probability/survival (Walds' $\chi^2 = 6.54$, $P = 0.012$, $df = 1$). Thus, the life history stage exposed to the most intense survival selection showed higher recapture rates of yearling pythons with lower parasitaemia compared to yearlings with higher parasite loads. Furthermore, in this truncated data set we did not detect any effect of body length on recapture probabilities (Walds' $\chi^2 = 0.09$, $P = 0.76$, $df = 1$). In order to investigate whether condition could affect yearling survival rates we expanded our model to incorporate this parameter. Again the only factor affecting recapture probabilities was parasite load (Walds' $\chi^2 = 5.40$, $P = 0.02$, $df = 1$), whereas neither body length, condition nor the interaction between parasite load and condition affected recapture rates (Walds' $\chi^2 = 0.00$, $P = 0.99$, $df = 1$; Walds' $\chi^2 = 2.01$, $P = 0.16$, $df = 1$; Walds' $\chi^2 = 1.76$, $P = 0.18$, $df = 1$, respectively).

Discussion

Most studies of parasite–host interactions have been based on correlative data (including the present study). However, in an elegant study of blue tits (*Parus caerulus*), Merino et al. (2000) were able to experimentally reduce the level of haematozoan infection using an anti-protozoan drug. The results from their study clearly demonstrated, and supported previous non-experimental findings of pathological effects of haematozoan infections on host life history traits such as condition and reproductive success (Merino et al. 2000). Consequently, although our results were not obtained by experimental manipulation of parasite infection level and, hence, there was no proof of causation, the effects on python fitness documented in the present study are supported by the experimental work of Merino et al. (2000).

Parasite prevalence among different host species and host populations often exhibits large variation (Apanius et al. 2000). In the present study, no infected erythrocytes were detected in 25 of the 329 stained blood samples examined. However, *Hepatozoon*-specific primers revealed that these snakes were indeed infected by the parasites (Ujvari et al. 2004). The prevalence of parasite infections in the water python population appears to be very high since examination of 100 randomly chosen samples all revealed *Hepatozoon*-specific polymerase chain reaction products (Ujvari et al. 2004).

Several studies of host–parasite interactions have reported parasite infection levels that vary both in time and space (e.g. Bensch and Åkesson 2003). However, results from the present study demonstrate that individual pythons maintained similar among-year parasite infection levels (Fig. 1), and mirror results obtained in other study organisms such as lizards (Sorci 1995) and birds (Duvfa 1996; Appleby 1999). The high degree of temporal stability of *Hepatozoon* infections in individual pythons suggests that the huge variation in parasite load observed among individual pythons may reflect their immune systems' ability to counteract parasite infections.

The majority of host–haematozoan interaction studies have been conducted on birds and mammals, most of which exhibit determinate growth. The comparatively fast juvenile growth rate in this group of animals may explain why only a small number of studies have reported effects of haematozoan infection on host growth rate. In a study of mallards (*Anas platyrhyncus*) and American black ducks (*A. rubripes*), Schutler et al. (1999) did not observe any effect of haematozoan parasites on duckling growth rate, whereas Soler et al. (2002) suggested that a high parasite load may have hampered growth in nestling magpies (*Pica pica*). Water pythons, like most other reptiles, exhibit indeterminate growth and, hence, continue to increase in body size even at an old age, albeit at a slower rate (e.g. Madsen and Shine 2000). Our results suggest that *Hepatozoon* infections had a dramatic impact on python growth rates, i.e. pythons suffering from a high infection level exhibited significantly slower growth compared to individuals with lower parasite loads (Fig. 2). What could be the cause of the negative relationship between parasite infection levels and python growth? Parasites that enter the erythrocytes cause physiological stress by destroying the cells and consuming the haemoglobin (Atkinson and van Riper 1991). In the common lizard (*Lacerta vivipara*), individuals infected by protozoans of the genus *Haemogregarina* had lower levels of haemoglobin, an increased number of immature erythrocytes, decreased oxygen consumption and reduced running speed (Oppliger et al. 1996). Furthermore, Oppliger and Clobert (1997) observed a significantly reduced tail regeneration rate in parasitized common lizards compared to non-parasitized individuals, and suggested that the difference in tail regeneration rate might have been due to a reduced metabolic rate caused by decreased haemoglobin levels. Consequently, we suggest that the negative effects of haematozoan parasite load on python growth rate may have been caused by a concomitant reduction in metabolic rates. Madsen and Shine (2000) demonstrated that juvenile pythons hatching during years with a low food supply grew significantly slower and never reached as large a body size as pythons hatching during years with a high food supply. However, at present we do not have sufficient long-term growth rate data on juvenile pythons, from which the parasite levels have been quantified, to enable us to investigate whether, not only

food supply, but also parasite infections, may have long-lasting effects on adult body size.

In their experimental approach to quantifying effects of haematozoan parasitaemia in blue tits, Merino et al. (2000) detected a significant parasite-dependent deterioration in the condition of control females but did not observe this in the medicated birds, strongly suggesting that the haematozoan parasites affected female nutritional status. A similar result is apparent in our study i.e. pythons with lower body condition scores suffered from higher levels of *Hepatozoon* infections (Fig. 3).

Like other snakes, female water pythons are capital breeders and consequently use stored energy reserves for egg development (Madsen and Shine 1996b). In order to reproduce, female pythons need to reach a more or less fixed ''reproductive threshold'' of stored energy reserves and consequently, reproductive females are heavier than their non-reproductive counterparts at the same body length (Madsen and Shine 1996a, 1999). The negative impact of parasitaemia on python nutritional status may, hence, reduce the ability of adult females to acquire sufficient fat body stores to reach such a reproductive threshold. Furthermore, several studies have presented data suggesting that haematozoan parasites affect female reproductive status (e.g. Dawson and Bortolotti 2001). Our results also suggest that parasites may have an impact on female reproductive output, since reproductive female pythons harboured lower parasite loads compared to non-reproductive females. Preliminary analyses of parameters affecting the population demography of the Fogg Dam water pythons suggest that number of reproductive females and juvenile survival (i.e. recruitment) constitute the main determinants in driving the dynamics of the python population (T. Madsen et al., in preparation). The negative impact of *Hepatozoon* parasite infections on both female reproductive output and juvenile survival strongly suggests that these parasites may play an important role in the demography of these tropical predators.

Several studies on passerine birds have reported that haemoparasite prevalence increases with advancing host age (Weatherhead and Bennet 1991; Allander and Bennet 1994; Norris et al 1994; Sanz et al. 2001). However, results from our study paint a different picture since parasite load was lower in larger/older pythons compared to younger snakes (Fig. 4), suggesting that only snakes harbouring lower levels of parasitaemia, were able to survive to an old age. What can explain the discrepancy between our results and those obtained in the studies cited above? The principal determinant in the evolution of longevity is predicted to be the level of extrinsic mortality, e.g. predation (Kirkwood and Austad 2000). If this level is high, life expectancy in the wild is short and selection for somatic maintenance will be low (Kirkwood and Austad 2000). Conversely, if the level of extrinsic mortality is low, selection is predicted to direct greater investment into maintaining a durable soma (Kirkwood and Austad 2000). Thus, evolutionary theories of longevity predict that self-maintenance functions, such as those of the immune system, will be selectively maintained when extrinsic sources of mortality are low relative to intrinsic sources. The immune system is an energetically expensive self-maintenance complex (e.g. Råberg et al. 2002). Thus, one would also expect the onset of immunosenescence to differ among animals with different life history strategies. Due to the their large size water python have very few natural predators and hence, experience low mortality rates and commonly reach an age of >15 years (Madsen and Shine 2000). Thus, a possible cause for the opposing results regarding parasite prevalence and host age among passerine birds and water pythons may be due to different levels of extrinsic mortality rates and, hence, longevity. Consequently, long-lived organisms, such as water pythons, may invest relatively more into crucial self-maintenance functions such as parasite defence, compared to short-lived passerine birds, and only individuals capable of such an investment will reach an old age.

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