

# Host–parasite coevolution: comparative evidence for covariation of life history traits in primates and oxyurid parasites

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## SUMMARY

The environmental factors that drive the evolution of parasite life histories are mostly unknown. Given that hosts provide the principal environmental features parasites have to deal with, and given that these features (such as resource availability and immune responses) are well characterized by the life history of the host, we may expect natural selection to result in covariation between parasite and host life histories. Moreover, some parasites show a high degree of host specificity, and cladistic analyses have shown that host and parasite phylogenies can be highly congruent. These considerations suggest that parasite and host life histories may covary. The central argument in the theory of life history evolution concerns the existence of trade-offs between traits. For parasitic nematodes it has been shown that larger body sizes induce higher fecundity, but this is achieved at the expense of delayed maturity. As high adult mortality would select for reduced age at maturity, the selective benefit of increased fecundity is expressed only if adult mortality is low. Parasite adult mortality may depend on a number of factors, including host longevity. Here we tested the hypothesis concerning the positive covariation between parasite body size (which reflects parasite longevity) and host longevity. To achieve this goal, we used the association between the pinworms (Oxyuridae, Nematoda) and their primate hosts. Oxyurids are highly host specific and are supposed to be involved in a coevolutionary process with their hosts. We found that female parasite body length was positively correlated with host longevity after correcting for phylogeny and host body mass. Conversely, male parasite body length and host longevity were not correlated. These results confirm that host longevity may represent a constraint on the evolution of body size in oxyurids, at least in females. The discrepancy between female and male oxyurids is likely to depend on the particular mode of reproduction of this taxon (haplodiploidy), which should result in weak (or even null) selection pressures to an increase of body size in males.

## 1. INTRODUCTION

Life history traits, such as age at first reproduction, fecundity and survival, show a tremendous degree of variation among organisms (Roff 1992; Stearns 1992). The central argument in the theory of life history evolution concerns the existence of trade-offs between traits (Roff 1992; Stearns 1992). These trade-offs set a limit to the possible options one individual has to produce propagules and persist over time (Sibley & Calow 1986). Although several debates have been raised about how to measure life history trade-offs (see Reznick 1985; van Noordwijk & de Jong 1986), both intra- and interspecific evidence supports the view that fecundity trades off against mortality (Partridge & Farquhar 1981; Harvey & Zammuto 1985; Gustaffson & Sutherland 1988; Saether 1988).

Coevolution indicates the reciprocal genetic changes of one or more traits occurring in two or more interacting species (Futuyma & Slatkin 1983). Coevolutionary processes are known to occur for a large spectrum of organisms, ranging from mutualistic to parasitic interactions (Futuyma & Slatkin 1983). In this context, we might expect that life history traits of these interacting species show a certain degree of covariation. The evolution of host life history traits in response to the pathogenic effect of parasites has recently received attention from both theoretical and experimental studies (Minchella 1985; Hochberg *et al.* 1992; Forbes 1993; Lafferty 1993; Sorci & Clobert 1995; Sorci *et al.* 1996). These studies have pointed out that under certain circumstances host life history evolution may be parasite driven. Similarly, recent work has focused on parasite life history evolution in response to host characteristics (mainly body size; see Poulin 1995 for a review), although much less information is available on parasite life histories compared to other organisms.

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Among metazoan parasites, nematodes represent one of the most suitable groups in which to study life history evolution. Skorping *et al.* (1991) and more recently Morand (1996) analysed life history trade-offs in 66 and 30 nematode species, including both parasitic and free-living species. These studies showed that prepatent period was positively correlated with female body length, and that prepatent period was negatively correlated with female adult mortality rate. In other words, longer growth periods induce larger body sizes, and high adult mortality selects for shorter maturation time. As larger body sizes may confer selective advantages in terms of increased fecundity, we might expect the evolution of large female size in parasitic nematodes. However, as noted before larger body size is attained at the expense of slower growth rates, and if adult mortality is high, this might not be the best strategy to adopt. This can be particularly true if host lifespan (or the period when the host is susceptible to parasite attacks) is not long enough. In this scenario, the evolution of parasite body length, and thus parasite adult life expectancy, might be constrained by host longevity (Keymer *et al.* 1991). Although this can seem paradoxical, we should point out that parasitic nematodes present a very wide variety of life history patterns. For instance, some species (e.g. *Trichinella spiralis*) start to reproduce after five days, whereas other species (e.g. *Strongylus edentatus*) have maturation times close to one year. Longevities also display large variation, and some species may be reproductively active for several years (e.g. *Necator americanus*, which has an adult life expectancy of more than six years; Morand 1996).

The question concerning a positive covariation between parasitic nematode body size and host longevity was firstly addressed by Harvey & Keymer (1991). They used the association between pinworms of the genus *Enterobius* (Oxyuridae) and their primate hosts. Although their sample size was quite small ( $n = 11$  species) they found that long-lived hosts significantly tended to harbour larger parasite species, and this correlation did not depend on host body size. In this paper, we aimed to test the hypothesis concerning the evolution of parasite life history traits in response to host longevity, by studying the same association used by Harvey & Keymer (1991) but with a larger data set ( $n = 35$  species). Moreover, we collected data on both female and male adult parasite body size. This allowed us to test any differential effect of host longevity on parasite body size between sexes.

## 2. METHODS

### (a) Data collection

Data on female and male body size were collected for 35 species of Oxyuridae. This information was extracted from Skrjabin *et al.* (1960). Estimates of primate longevity (maximum recorded lifespan) and body mass were taken from Harvey *et al.* (1987).

### (b) Biology of Oxyuridae

Pinworms are common parasites of New and Old World primates. They usually show a high host-specificity and

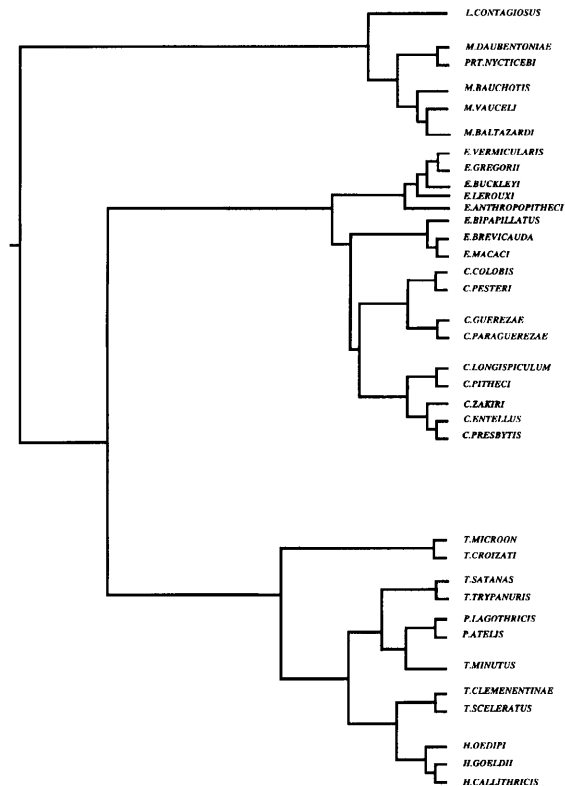


Figure 1. Oxyurid phylogeny used in the study. The genera are *Lemuricola* (L), *Madoxyuris* (M), *Protenterobius* (PRT), *Enterobius* (E), *Colobenterobius* (C), *Trypanoxyuris* (T), *Paraoxyuronema* (P), *Hapaloxoyuris* (H).

cladistic studies have provided evidence for a coevolutionary relationship between oxyurid parasites and their primate hosts (Brooks & Glen 1982; J.-P. Hugot, in preparation).

Pinworms have a direct life cycle. Adult worms inhabit the digestive tract of the host, where they are attached to the mucosa of the large intestine. When females become gravid, they detach and move towards the anus, where eggs are laid. Outside the host, the embryonic development goes on to the second juvenile stage, when reinfection can occur. After being ingested by a new host the egg hatches, and the juvenile completes two more moults in the host digestive tract, before attaining the adult stage (Anderson 1992).

### (c) Statistical analysis

We used Felsenstein's contrast method (Felsenstein 1985) to test the correlation between parasite body size and host longevity. The contrasts were computed using phylogenetic information on pinworms contained in J.-P. Hugot (in preparation) (figure 1). We calculated statistically independent linear contrasts between taxa and tested whether a change in body size was associated with a change in host longevity. This was done for female and male body size. All variables were  $\log_{10}$ -transformed. The contrasts were standardized assuming that the time since divergence of taxa was directly proportional to the number of taxa. The contrasts were computed using the CAIC statistical package (Purvis & Rambaut 1994, 1995). All details of the method of calculation are given therein. We used a linear regression model to test whether an evolutionary change in parasite body length was associated with a change in host longevity. The regression models were always forced through the origin. As host body mass may represent a confounding variable, potentially correlated with both parasite body size and host longevity, we included this variable in the regression model.

### 3. RESULTS

Both female and male oxyurid body length showed a large degree of variation ranging from 2.85–10.13 mm for females ( $n = 35$ ) and from 1.20–3.85 mm for males ( $n = 33$ ). In all species, females had larger body sizes than males ( $n = 33$ ) and the female biased size dimorphism (female length over male length) ranged from 1.68–6.14. Contrasts of female and male body length were positively correlated (slope  $\pm$  s.e.,  $b = 0.545 \pm 0.113$ ,  $F_{1,30} = 23.43$ ,  $p < 0.001$ ; figure 2).

Female parasite body length was positively correlated with host longevity after controlling for phylogeny and host body mass ( $b = 0.400 \pm 0.154$ ,  $F_{1,31} = 6.74$ ,  $p = 0.014$ ; figure 3). Conversely, host longevity was not a significant predictor of male parasite body length ( $b = 0.350 \pm 0.220$ ,  $F_{1,28} = 2.54$ ,  $p = 0.123$ ; figure 4).

To test if relative female body size (after correcting for male body size) was also positively correlated with host longevity, we regressed female body length on male body length and computed the residuals. These residuals were then regressed on the residuals of the regression of host longevity on host mass. The slope of the regression of residual female body size on residual host longevity was positive but not statistically significant ( $b = 0.213 \pm 0.128$ ,  $F_{1,28} = 2.76$ ,  $p = 0.108$ ).

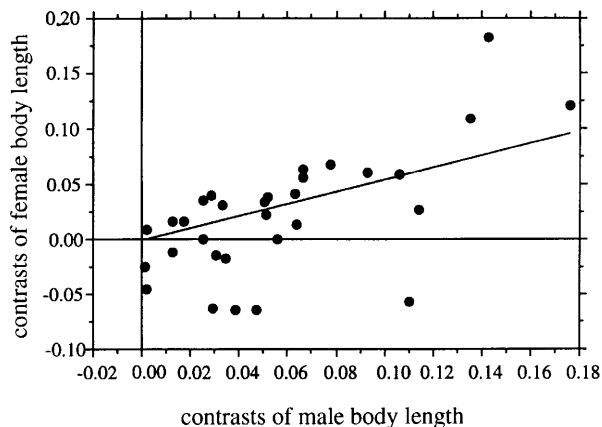


Figure 2. Regression through the origin of female body length on male body length. Each point represents an independent contrast.

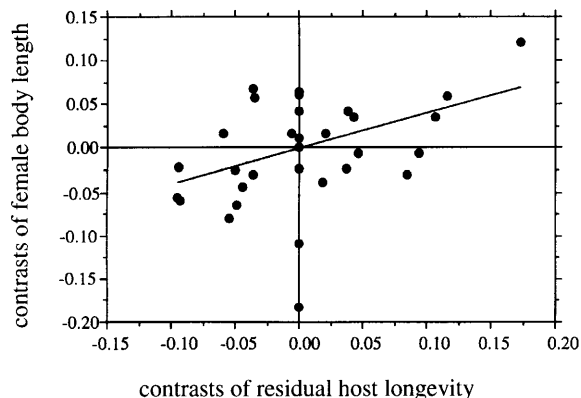


Figure 3. Regression through the origin of female body length on residual host longevity. Each point represents an independent contrast.

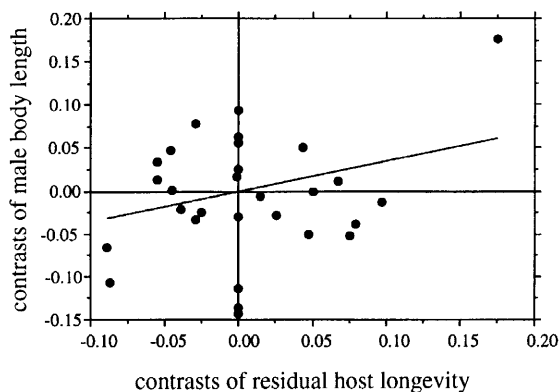


Figure 4. Regression through the origin of male body length on residual host longevity. Each point represents an independent contrast.

### 4. DISCUSSION

We found a positive association between female oxyurid body length and longevity of their primate hosts. Oxyurid male body length, which is significantly smaller than in females, was not correlated with host longevity. These results are in good agreement with those reported by Harvey & Keymer (1991), who, using a reduced number of pinworm species, also showed a positive association between parasite size and primate longevity. This finding also supports the hypothesis that oxyurid body size, at least in females, evolves in response to the longevity of their hosts.

The evolution of large body size in females has generally been supposed to depend on the fecundity advantage of larger individuals (Shine 1988, 1989; Keymer *et al.* 1991). This may be particularly true for organisms with undetermined growth, such as nematodes, which continue to grow even after having attained sexual maturation. However, if large sizes confer a fecundity advantage, why are not all species equally big? The evolution of large body size is likely to depend on two life history traits, growth rate and age at first reproduction (equivalent to prepatent period in parasitic species). Long growth periods usually result in large body size and delayed maturity. The fecundity benefit of large size is therefore traded off against a delayed maturity (Stearns 1992). If mortality rates are high, the best demographic strategy might not be to wait a long time to breed for the first time, and this can represent a strong selective force against an evolutionary increase in body size.

Heterogeneous environments result in variable selective forces acting on organisms, and consequently natural selection may favour genotypes with locally adapted phenotypes. This is certainly true for free-living and parasitic species, with the difference that the principle environmental characteristics for a parasitic species are provided by the host itself. Therefore, as the aspects of host environment most likely to affect parasite life history (such as resource availability and immune responses) are well characterized by the life history of the host, we may expect natural selection to result in covariation between parasite and host life histories. Nematodes and primates provide a good example to study life history covariation in parasites

and their hosts. The high host specificity and the congruence between the pinworm and primate phylogenies strongly suggest that the two groups are involved in a coevolutionary process (Brooks & Glen 1982; J.-P. Hugot, in preparation). Moreover, the life cycle of pinworms, which does not require the presence of an intermediate host, makes it easier to predict the patterns of covariation between life histories. Finally, although we do not know much about the longevity of oxyurids, knowledge of adult life expectancies of parasitic nematode species indicates that adult lifespan may reach levels comparable to that of their hosts (Maizel *et al.* 1993; Morand 1996).

Patterns of nematode infections may vary considerably from one species to another, and the immune response elicited by nematodes on their hosts is also likely to depend on the number of parasites present in the host (Anderson 1982). As a consequence, some species can persist in the host for most of its lifespan, whereas some other species, such as *Enterobius vermicularis* in humans, are only encountered in young hosts. Although some species are only present during a short period of the entire lifespan of a given host, our analysis can provide a useful insight into the relationship between host and parasite life histories, because the duration of the susceptible stage in hosts (e.g. from birth to sexual maturity) is likely to be positively correlated with total longevity (Harvey & Zammuto 1985).

At the opposite of female parasite body length, male body size was not positively correlated with host longevity. Why does this discrepancy between sexes occur? As previously noted, a large body size confers a selective advantage to females through an increase in reproductive output. As male gametes are produced in very large numbers and are extremely small-sized, males usually do not benefit from a direct 'fecundity' advantage of having a large body size. Other selective forces can, however, induce an evolutionary increase of body size in males (Shine 1989). These selective forces rely on the intrasexual competition for mates, and this argument has been evoked to explain the evolution of male-biased sexual dimorphism in mammals (Cope's rules; McLain 1993). Oxyurids present a particular system of reproduction. Males develop from unfertilized eggs and are thus haploid, whereas females develop from fertilized eggs and are diploid (Adamson 1989). A persistent component of haplodiploidy across different taxa is an elevated level of inbreeding (Hamilton 1967; Borgia 1980), which implies that within-host populations usually consist of closely related parasite individuals. Haplodiploidy may also favour the evolution of female-biased sex ratios because of both local mate competition and kin selection (Hamilton 1967; Wilson & Colwell 1981; May & Seger 1985), with the consequence that males are produced in minimum number to ensure egg fertilization. These two considerations, kin selection and local mate competition, should reduce the intensity of selection pressures favouring males with larger body sizes. In summary, given the particular system of reproduction of Oxyurida, male body size does not seem to be under strong selection to increase in

evolutionary time, and this in turn can account for the lack of correlation between male body size and host longevity.

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