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# Cost of reproduction and cost of parasitism in the common lizard, *Lacerta vivipara*

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Parasites may play a complex role in shaping patterns of host reproductive effort and therefore in determining costs of reproduction in their hosts. Parasites may cause a more or less large reduction in the amount of energy an individual host may use for reproduction and maintenance. Irrespective of the parasite-induced reduction in energy intake, infected hosts may either show the same allocation pattern than uninfected hosts, or respond to parasitism by changing the proportion of energy allocated to each trait (e.g. increased investment in current reproduction at the expense of survival). Moreover, hosts may differ in their susceptibility to parasites (e.g. hosts with high reproductive effort may show higher vulnerability to parasite infection). Each of these hypotheses leads to a pattern of correlation between parasite load, host survival and reproduction. In this paper we compared the predicted patterns of correlation between parasite load, host survival and reproduction with those observed for the *Lacerta vivipara* – haematozoa association. We found that: (1) haematozoa load was positively correlated with lizard reproductive effort; (2) haematozoa load was not correlated with host survival; (3) lizards with high reproductive investment suffered higher mortality rate than lizards with low reproductive investment. These findings suggest that parasites do not significantly reduce host energy intake, and are in agreement with a shift of the allocation rule of parasitized hosts toward reproduction. However, our correlative study does not allow us to attribute this shift to an adaptive host response to parasites rather than a by-product of a differential susceptibility to parasite infections.

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Life-history theory assumes that organisms cannot increase the allocation of limited resources to reproduction without diverting a proportional amount of energy from another life-history trait (Sibly and Calow 1986, Calow 1987, Roff 1992, Stearns 1992). This allocation principle implies that life-history traits cannot evolve independently. In particular, selection pressures favouring an increase in fecundity will cause a decrease in some other fitness components (Roff 1992, Stearns 1992).

The cost of reproduction is one of the best studied trade-offs involving life-history traits, indicating the decrease in survival or future fecundity which can be imputed to a given reproductive event (Williams 1966, Bell 1980, Reznick 1985, 1992, Bell and Koufopanou 1986). Several studies conducted on different groups of organisms have contributed to elucidate how the cost of reproduction can shape energy allocation among life-history traits (Gustafsson and Sutherland 1988, Nur 1988, Pettifor et al. 1988, Gustafsson and Pärt 1990, Schwarzkopf 1993, 1994). Four methods have been extensively used to study the cost of reproduction (Reznick 1985): phenotypic correlations between reproductive investment and survival in natural populations provided contradictory results and have been criticised by some authors (Reznick 1985, van Noordwijk and de Jong 1986); experimental manipulation of reproductive

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investment may be a very useful tool to study the causal relationship between reproductive effort and survival (Nur 1988, Pettifor et al. 1988, Gustafsson and Pärt 1990); genetic correlations indicate to what extent a change in reproductive expenditure will determine a change in longevity (Rose and Charlesworth 1981a); finally artificial selection allows one to observe the amplitude of the change on longevity as a consequence of a change on reproductive effort (Rose and Charlesworth 1981b). Unfortunately, although the third and the fourth methods are by far the most unequivocal way to assess the cost of reproduction, their suitability to study natural populations is poor.

Parasites may play a complex role in shaping patterns of host reproductive effort and therefore in determining the cost of reproduction in their hosts (Møller 1993, in press). By reducing energy available for host physiological pathways, parasites may exert strong selective pressures on their hosts. Infected hosts can thus show altered patterns of resource allocation driven by parasites. A typical consequence of parasite-induced reduction in energy available for host reproduction is that infested hosts exhibit lower fecundity (Moss and Camin 1970, Schall 1983, Møller 1990, Keymer and Read 1991, Richner et al. 1993). On the other hand, changes in the pattern of resource allocation can be host-driven, and can correspond to an adaptive response to parasite-induced fitness costs (Forbes 1993).

In this paper we investigated the relationships between parasite load and host resource allocation between current reproduction and survival. We first derived predictions, using a graphical model, on the correlation between parasite load, host reproduction and host survival. Using the common lizard–haematozoa association we tested if the level of parasite infestation was correlated with reproduction and survival, and if infected hosts showed any of the possible patterns predicted by life-history theory. We used this association because lizards are convenient organisms for the study of the cost of reproduction and the cost of parasitism. Many lizard species rely for reproduction and survival on resources stored as fat and therefore any factor depleting these fat reserves might affect life-history traits (Schwarzkopf 1994). Furthermore, haematozoa have been shown to play a central role in diverting energy from reproduction in some lizard species (Schall 1983).

## A graphical model

To illustrate the possible interactions between parasitism and host resource allocation, we will refer to life-history theory on trade-offs. We assume that there is a trade-off between survival and reproduction so that when individuals of only one category are considered there is a negative correlation between these two traits. Two factors are going to affect the sign of the correlations between parasite load, host reproduction and host survival. These are the parasite induced reduction in host energy intake and the possibility that hosts may alter their resource allocation pattern subsequent to infection. Fig. 1 represents trade-off curves between current reproduction and survival for infected and uninfected hosts, according to different rules of host resource allocation. For simplicity, suppose that uninfected hosts have a maximum energy intake equal to 100 units which they allocate equally to current reproduction and maintenance. Parasites may either cause a substantial reduction of this initial energy (e.g. only 50 units of energy are available to individual hosts; Fig. 1A and B), or have a small effect on host initial energy (e.g. only 90 units of energy are available to individual hosts; Fig. 1C). Within each of these pathways infected hosts may either follow the same allocation rule as uninfected hosts (Fig. 1A and C), or change the proportion of energy allocated to each trait (Fig. 1B and D) (we assume that in this case infected hosts increase investment in current reproduction at the expense of survival). Whatever the amount of host energy reduction caused by parasites, if hosts do not change their allocation rule, parasitism would negatively affect host fitness (Fig. 1A, B, and C). On the other hand, if parasites induce only minor reductions in energy intake hosts may offset parasite-induced survival costs by increasing their current reproductive investment (Fig. 1D).

For each of these patterns of resource allocation, we can predict the relationships between survival, reproduction and parasite load when one analyses both infected and uninfected individuals. For example, the pattern of resource allocation represented in Fig. 1A leads to: (1) positive correlation between survival and reproduction; (2) negative correlation between parasite load and survival; (3) negative correlation between parasite load and reproduction. The positive correlation between reproduction and survival arises here because of the large differences between infected and uninfected individuals (van Noordwijk and de Jong 1986, de Laguerie et al. 1991). The scenario of Fig. 1D leads to (1) negative correlation between survival and reproduction; (2) negative correlation between parasite load and survival; (3) positive correlation between parasite load and reproduction. Table 1 gives the expected sign of the correlations among the three traits under the different scenarios.

All of the previous examples assume that hosts have equal probabilities to encounter and to sustain parasites. However, recent experimental evidence shows that hosts with high reproductive investment are more susceptible to parasitism than hosts with low reproductive effort (Norris et al. 1994, Richner et al. 1995). Therefore positive correlations between parasitism and host reproduction may simply reflect a by-product due to

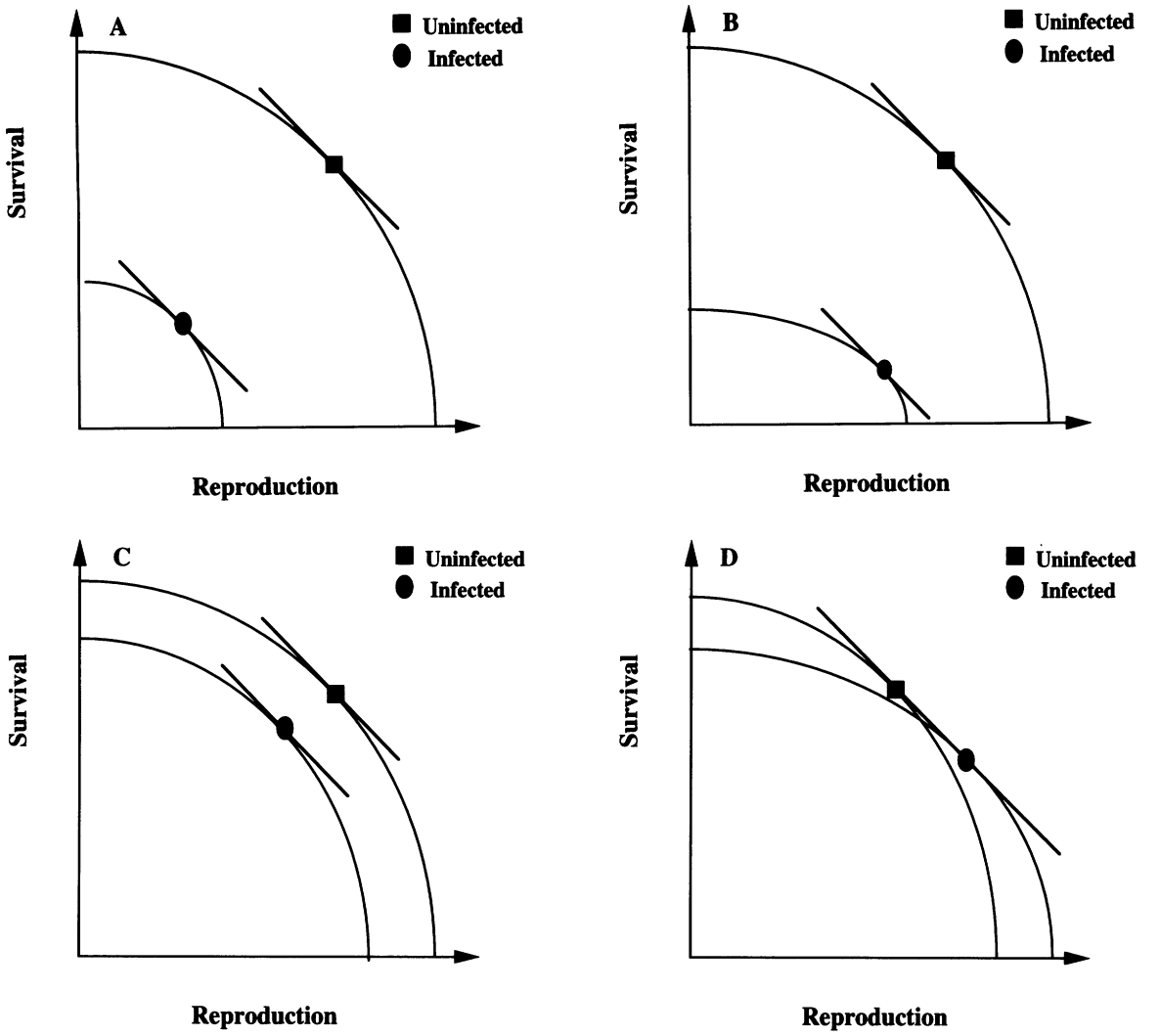


Fig. 1. Trade-off curves between current reproduction and survival. Straight lines represent isoclines of fitness. Fitness is maximised at the point where the fitness isocline is tangent to the trade-off curve here represented by squares and dots for uninfected and infected hosts respectively (Roff 1992). Figures A and D illustrate different patterns of parasite-induced reduction in host energy intake and host resource allocation rules: (A) large parasite-induced reduction in host energy intake and same resource allocation rule between uninfected and infected hosts; (B) large parasite-induced reduction in host energy intake and different resource allocation rule between uninfected and infected hosts; (C) low parasite-induced reduction in host energy intake and same resource allocation rule between uninfected and infected hosts; (D) low parasite-induced reduction in host energy intake and different resource allocation rule between uninfected and infected hosts. (D) also illustrates the case where uninfected and infected hosts lie on the same fitness isocline but have different susceptibility to parasites.

poor physiological conditions of hosts with high reproductive effort, rather than host adaptation to offset the cost of parasitism. Fig. 1D represents trade-off curves for infected and uninfected hosts assuming that susceptibility to parasites differs between groups. Infected hosts have higher reproductive effort and lower survival than uninfected hosts, but equal fitness as they lie on the same fitness isocline.

We can summarize the predictions of this simple graphical model as follows: (1) if hosts do not change their allocation rule, parasitism would negatively affect host fitness whatever the amount of host energy reduction caused by parasites; (2) if parasites largely reduce the amount of energy that hosts may use for their reproduction and maintenance a positive correlation arises between host survival and reproduction; (3) if the reduction in host energy intake induced by parasites is small and hosts modify their allocation rule (i.e. increasing their current reproductive investment), then parasites might not have negative effects on host fitness, resulting in a positive correlation between parasite load and reproductive effort; (4) positive correlations between host reproductive effort and parasite load may arise only if infected hosts bias their resource allocation towards reproduction, the parasite induced reduction in host energy intake being small, or if hosts differ in their

Table 1. Predicted sign of the correlation between host reproductive effort (R), host survival (S) and parasite load (P) under different hypotheses on the magnitude of the parasite induced reduction of host energy intake and the potential for hosts to alter their allocation pattern following an infection. The predictions assume that both infected and uninfected individuals are analysed. In all cases where two signs are given for the correlation between two traits, the first sign is the prediction of the graphical model. The second sign reflects the possible outcome of the experimental measure of these correlations if the variance of these traits is large.

| | | S-R | S-P | R-P |
|---|---|---|---|---|
| large reduction | no shift in allocation pattern | + | − | − |
| | allocation pattern changed | + | − | − or 0 |
| minor reduction | no shift in allocation pattern | − | − or 0 | − or 0 |
| | allocation pattern changed | − | − or 0 | + |

vulnerability to parasite infection as a function of their reproductive investment.

These predictions might be slightly modified if the various factors have only a weak influence on the shaping of the traits (i.e. if inter-individual variability is very large). In that case correlations predicted to be negative could be null.

In the light of these predictions we measured in the field correlations between parasite load, reproductive investment and survival using the common lizard–haematozoa association.

## Materials and methods

### The species

The common lizard (*Lacerta vivipara*) is a live-bearing lacertid living in peatbogs and heathland. Adult snout-vent length ranges from 50 to 70 mm. A variable proportion of females became sexually mature when two-year-old, whereas almost 100% of the population reproduces by three years of age (Massot et al. 1992). Mating takes place in May, parturition beginning two months later. Females lay 5 (min–max 1–12) shell-less eggs which hatch immediately after being laid. The average lifespan is five years, although some individuals can exceptionally live more than ten years (pers. obs.). A more complete description of the life cycle can be found in Pilorge (1987).

### Lizard collection and maintenance

At the beginning of July 1992 and 1993 we captured 168 and 163 gravid females respectively, at four study sites in southern France. The four plots (A, B, C, D) are located within an area of 4.1 km$^2$ in Mont Lozère (44° 30′ N, 3° 45′ E).

At capture time, we recorded snout-vent length (SVL), and body mass. Females were then maintained in a field laboratory until they gave birth. Females were individually housed in plastic terraria (15 × 20 × 15) with damp soil, a shelter, water ad libitum, and were fed with larvae of *Pyralis farinalis*. They were exposed to natural daylight and were kept warm 6 h per day with a gradient of 25 to 30°C. Females were checked twice a day for parturition. For each post-parturient female we recorded litter size, female body mass, and juvenile body size and mass. Then, females were released at the site where they had been captured, and were followed by recapture techniques in the following years. We conducted two recapture sessions per year: May–June, and July–August which allowed us to estimate survival rates.

### Parasite sampling

Gravid females were sampled for haematozoa parasites by collecting a smear with blood from the tip of the tail; smears were air dried, fixed in absolute ethanol and stained with Giemsa stain. Haematozoa were quantified by counting the number of parasites in 25 successive fields under oil at magnification 1000×. We considered the percentage of parasitized blood cells per slide as an estimate of lizard parasite load. We also computed the prevalence for each plot as the percentage of parasitized individuals (Margolis et al. 1982). All haematozoa found in the blood smears belonged to the family Haemogregarinidae.

### Defining reproductive investment

We used three different variables to measure female reproductive investment: litter size (LS), relative clutch mass (RCM), and investment per young (INV). We defined RCM as the difference between female mass before and after parturition divided by female mass before parturition. Investment per young was the difference between female mass before and after parturition divided by litter size. RCM gives an overall estimate of female relative investment in reproduction, whereas INV gives an estimate of female relative investment in each offspring.

## Statistical analyses

As parasite load distribution was highly skewed, we log(+1) transformed this variable. Differences in prevalence among plots and years were estimated using a log-linear model. We used parametric statistics (ANCOVA) to test the correlation between reproductive investment and parasite load, after having checked for the assumptions underlying the linear models (Sokal and Rohlf 1981). In reptiles, reproductive parameters generally depend on snout-vent length. To remove the potential confounding effect of this variable, we included it in the model as a covariate. Therefore, the statistical model used was: $Y = \mu + \text{plot} + \text{year} + \text{parasite load} + \text{SVL} + \text{interactions} + \varepsilon$. We used the Type III SS (PROC GLM, SAS Release 6.4, SAS Institute, 1990) for hypothesis testing because: (1) it is invariant to the ordering of effects in the model; (2) it tests the same hypothesis that would be tested if the data were balanced. To select the final model, we started with the complete one, and we successively dropped, step by step, all the non-significant interactions.

One of the most serious problems one faces when studying survival in natural populations, is that unrecaptured individuals cannot be surely considered as being dead. Individuals displaying particular behaviours (e.g., reduced activity levels) may avoid capture, resulting in lower apparent survival. In other words, we need to distinguish the survival rate from the capture rate if we want to have reliable information on selection pressures acting on a particular trait. To solve this problem, survival and recapture rates were estimated using the Cormack-Jolly-Seber model (Clobert and Lebreton 1987). We used the program SURGE4 (Pradel et al. 1990) to fit models. The models were compared by log-likelihood ratio tests (Clobert et al. 1987, Lebreton et al. 1992, 1993). However, SURGE4 can only handle categorical variables. Therefore, to transform relative clutch mass and investment per young we computed the mean of each character and we grouped individuals in two classes corresponding to lower RCM than the population mean or to higher RCM than the population mean. Since the distribution of parasite load was skewed we could not follow the same reasoning for this variable. We could not pool parasitized vs unparasitized individuals either, since the very high prevalence (see Results) made the sample sizes in each class too unequal. Therefore, we decided to consider lizards with less than 1% of parasitized blood cells (p0) vs lizards with more than 1% of parasitized blood cells (p1). The survival analysis was carried out only for plot B, because this was the site where the recapture effort and the initial sample size were the highest.

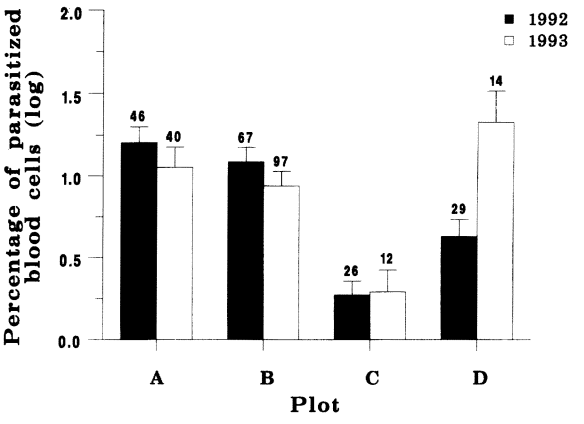


Fig. 2. Among-plots and between-years variability in parasite load. Bars represent standard errors. Sample sizes are given above the bars.

## Results

Prevalence was very high for plots A, B, and D in both years (1992: A, 97.8%, $n = 46$; B, 91%, $n = 67$; C, 42.3%, $n = 26$; D, 72.4%, $n = 29$; 1993: A, 77.5%, $n = 40$; B, 74.2%, $n = 97$; C, 33.3%, $n = 12$; D, 92.9%, $n = 14$). Prevalence differed significantly among plots, and the interaction between year and plot was also significant (log-linear model: plot, $\chi^2_3 = 32.69$, $p < 0.001$; year, $\chi^2_1 = 2.15$, $p = 0.143$; plot × year, $\chi^2_3 = 8.45$, $p = 0.038$). Prevalence decreased in plots A, B, and C, while it increased in plot D. The same pattern was found for parasite load, expressed as the percentage of parasitized blood cells (Fig. 2) We found a significant plot effect on parasite load as well as the interaction between year and plot (two-way ANOVA: plot, $F_{3,323} = 11.13$, $p < 0.001$; year, $F_{1,323} = 1.06$, $p = 0.304$; plot × year, $F_{3,323} = 3.66$, $p = 0.013$).

### Correlation between parasite load and reproductive investment

Litter size was correlated with plot, year, and SVL. The interactions plot × year, and SVL × year were also significant. Litter size was not significantly associated with parasite load (Table 2). Concerning RCM, parasite

Table 2. Analysis of covariance of the relationship between litter size and parasite load controlling for plot, year, and snout-vent length (SVL).

| Source | DF | $F$ | $p$ |
|---|---|---|---|
| Plot | 3 | 3.05 | 0.029 |
| Year | 1 | 11.74 | <0.001 |
| Parasite load | 1 | 0.26 | 0.608 |
| SVL | 1 | 122.66 | <0.001 |
| Plot × Year | 3 | 6.86 | <0.001 |
| Year × SVL | 1 | 11.09 | <0.001 |
| Error | 296 | | |

Table 3. Analysis of covariance of the relationship between relative clutch mass (RCM) and parasite load controlling for plot, year, and snout-vent length (SVL).

| Source | DF | $F$ | $p$ |
|---|---|---|---|
| Plot | 3 | 0.42 | 0.740 |
| Year | 1 | 0.36 | 0.546 |
| Parasite load | 1 | 5.39 | 0.021 |
| SVL | 1 | 33.99 | <0.001 |
| Plot × Year | 3 | 6.50 | <0.001 |
| Error | 286 | | |

load, SVL, and the interactions plot × year were significant predictors (Table 3). Parasite load was positively correlated with relative clutch mass (slope ± se = 0.014 + 0.006, $p = 0.021$; Table 3). Investment per young was also associated with parasite load, SVL, and the interaction plot × year. Moreover, investment per young differed among plots (Table 4). As for RCM, INV was positively correlated with parasite load (Fig. 3). Therefore, females with high parasite load invested more in overall reproduction and invested more per young than females with low parasite load.

### Correlation between parasite load and survival

The survival rate of p0 lizards (53.8%) did not significantly differ from the survival rate of p1 individuals (51.0%) (log-likelihood ratio test: parasitism group $\chi^2_1 = 0.065$, $p = 0.800$). Interestingly, recapture rates differed between the two groups according to the recapture period (spring–summer) (log-likelihood ratio test: parasitism group × recapture period, $\chi^2_1 = 6.619$, $p = 0.010$). p0 lizards were significantly more captured than p1 individuals (Fig. 4).

### Correlation between reproductive investment and survival

Females with higher RCM experienced higher mortality rates than females with small reproductive investment in both recapture periods (Fig. 5) (log-likelihood ratio test: parasitism group, $\chi^2_1 = 4.932$, $p = 0.036$). Female recapture rates did not differ according to RCM (log-likelihood ratio test: RCM, $\chi^2_1 = 1.216$, $p = 0.271$). In turn, investment per young was correlated neither to survival nor to recapture rate (survival rate: log-likelihood ratio test, $\chi^2_1 = 0.234$, $p = 0.629$; recapture rate: log-likelihood ratio test, $\chi^2_1 = 1.766$, $p = 0.184$).

Table 4. Analysis of covariance of the relationship between investment per young and parasite load controlling for plot, year, and snout-vent length (SVL).

| Source | DF | $F$ | $p$ |
|---|---|---|---|
| Plot | 3 | 4.67 | 0.003 |
| Year | 1 | 1.26 | 0.262 |
| Parasite load | 1 | 10.39 | 0.001 |
| SVL | 1 | 9.97 | 0.002 |
| Plot × Year | 3 | 7.31 | <0.001 |
| Error | 283 | | |

## Discussion

Life-history theory on trade-offs together with patterns of resource allocation and parasite energy requirements allow predictions on the relationships between parasitism, host reproductive effort and survival. These predictions can be summarized as follows: (1) if hosts do not change their allocation rule, parasitism would reduce host fitness whatever the amount of host energy reduction caused by parasites; (2) if parasites largely reduce the amount of energy that hosts may use for their reproduction and maintenance a positive correlation arises between host survival and reproduction; (3) if the reduction in host energy intake induced by parasites is small and hosts modify their allocation rule (i.e. increasing their current reproductive investment), then parasites might not have negative effects on host fitness, resulting in a positive correlation between parasite load and reproductive effort; (4) positive correlations between host reproductive effort and parasite load may arise only if infected hosts bias their resource allocation towards reproduction, the parasite-induced reduction in host energy intake being small, or if hosts differ in their vulnerability to parasite infection as a function of their reproductive investment.

Our results allow us to reject the first two hypotheses. We found that: (1) parasite load was positively correlated with both female relative clutch mass and investment per young; (2) parasite load was not correlated with lizard survival; (3) relative clutch mass was negatively correlated with survival. Parasites affected host recapture rate and thus probably their level of activity.

### Cost of reproduction in lizards

We found a trade-off between relative clutch mass and survival. Females with high reproductive effort suffered higher mortality than females with low reproductive effort. This result suggests that energy is channelled in a given reproductive event at the expense of individual maintenance. This also suggests that potential inter-individual differences in the ability to acquire resources are weak enough not to mask the trade-off between reproductive effort and survival. Inter-individual variability in energy acquisition would have been indicated by a positive correlation between reproduction and survival, the best individuals in acquiring energy having both higher survival probabilities and reproductive effort (van Noordwijk and de Jong 1986, de Laguerie et al. 1991).

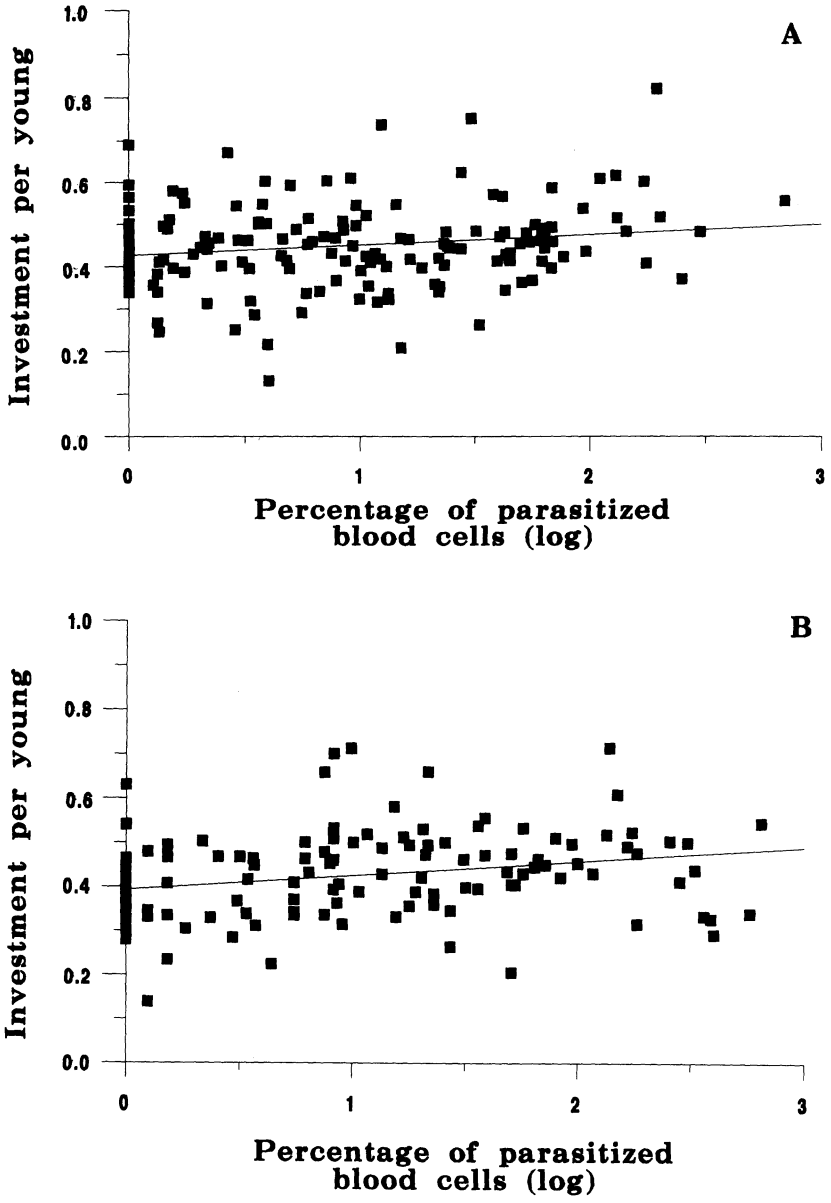


Fig. 3. Positive correlation between female investment per young and parasite load (A = 1992; B = 1993).

Costs of reproduction, expressed as survival costs, have been reported for several organisms, using both correlative and experimental procedures (Gustafsson and Sutherland 1988, Nur 1988, Pettifor et al. 1988, Gustafsson and Pärt 1990). Schwarzkopf (1993), for instance, showed that in female southern water skinks (*Eulamprus tympanum*) survival rate decreased as reproductive frequency increased.

Various physiological and/or behavioural changes associated with reproduction can be responsible for survival costs in lizards. These mechanisms include: (1) fat store depletion which may reduce energy allocated to maintenance (Derickson 1976); (2) increased basking during gestation (Bauwens and Thoen 1981) which may increase risks of predation during basking (Schwarzkopf and Shine 1991); (3) reduced escape abilities due to the egg burden (especially true for viviparous species, such as *Lacerta vivipara*) which may increase risks of predation (Bauwens and Thoen 1981, Brodie 1989); (4) increased vulnerability to parasites and diseases (Schall 1983). All of these possible mechanisms can account for the observed cost of reproduction in the common lizard.

## Cost of parasitism

We did not find evidence for a direct effect of parasitism on lizard survival. However, we showed that capture probabilities differed according to parasite load. This difference in capture rate suggests a difference in behaviour between the two parasitism groups,

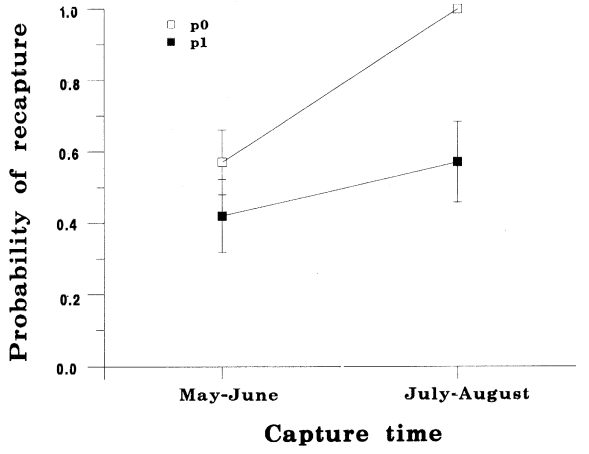


Fig. 4. Effect of parasitism level on host probability of recapture during spring and summer. White squares represent individuals with less than 1% of parasitized blood cells, black squares represent individuals with more than 1% of parasitized blood cells (see Methods). Bars represent standard errors.

but we do not know if these changes in behaviour may have some fitness repercussion for the parasitized individuals.

It could also be possible that parasites have a negative additive effect over time and that only older hosts suffer a direct survival cost. This hypothesis requires that levels of infestation stay relatively constant over time for a given individual. Indeed, we found a high repeatability of haematozoa load between years (Sorci 1995). To test the effect of parasites on older host survival would require to take into account the age structure of the host population.

Our findings of a lack of direct survival cost due to haematozoa are in contrast with other studies which showed a negative correlation between malaria infection and host survival (Richner et al. 1995). Schall (1983), for instance, reported lower survival rates for *Sceloporus occidentalis* lizards infected with *Plasmodium mexicanum* in laboratory conditions.

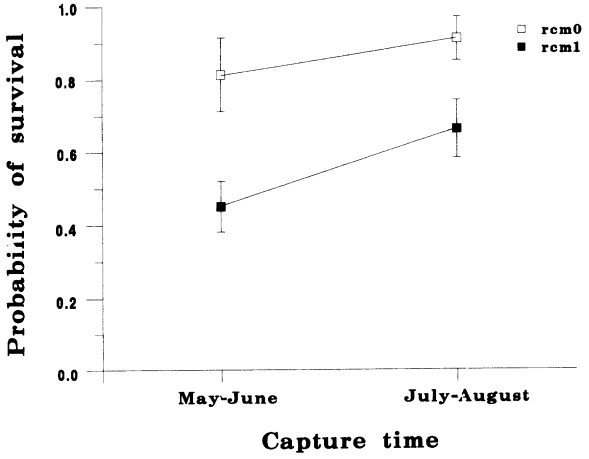


Fig. 5. Effect of reproductive investment on host probability of survival during spring and summer. White squares represent individuals with reproductive investment below the mean, black squares represent individuals with reproductive investment above the mean (see Methods). Bars represent standard errors.

## Parasitism and host reproductive effort

We found a positive correlation between haematozoa load and host reproductive effort. This result is in disagreement with the prediction that haematozoa reduce energy available to reproduction in the common lizard.

One could wonder to what extent the temporal dynamics of the host–parasite interaction can affect and determine the observed correlation between parasite load and reproductive effort. However, we found that parasite load stayed relatively constant between years in three out of the four studied populations, and the year as well as the population effects were factored out in each statistical analysis. Moreover, as noted before, haematozoa levels are repeatable between years in the common lizard, suggesting that parasitism is a predictable trait over time (Sorci 1995).

Two different pathways can lead to positive correlations between level of parasitism and host reproductive effort. First, high reproductive investment can be an adaptation to parasite infections. Some theoretical as well as empirical studies have emphasized the possible role of host life history modifications as a response to virulent parasites (Minchella and LoVerde 1981, Minchella 1985, Hochberg et al. 1992, Forbes 1993, Lafferty 1993, Sorci and Clobert 1995). For example, *Biomphalaria glabrata* snails suffer dramatic fecundity losses when infected by schistosomes; however, snails exposed to infective stages have higher fecundity during a short period after infection than unexposed snails (Minchella and LoVerde 1981). Higher fecundity after infection has been considered as a host response to offset the parasite-induced castration (Minchella 1985). Positive correlations between parasite load and host reproductive effort are also expected when parasites have a severe impact on host survival. If parasitized hosts have a low probability to survive until the subsequent reproductive event, selective benefits should exist for individuals maximising their investment in current reproduction.

The second pathway that may lead to a positive correlation between parasites and reproductive effort involves reduced anti-parasite immune defence of females with high reproductive investment. Supportive evidence to this hypothesis comes from the findings of negative relationships between immune defence and reproductive investment (see Møller in press, for a review). Other experimental studies showed that the

susceptibility to parasites was higher for hosts with high reproductive effort (Norris et al. 1994, Richner et al. 1995).

Our correlative study does not allow us to assess to what extent the positive correlation between parasite load and host reproductive effort is an adaptive response of the host to parasite infection or the consequence of a higher susceptibility to parasites of hosts with high reproductive effort. To provide conclusive evidence will necessitate experimentally manipulating parasite load and host reproductive effort. Since manipulation of host reproductive effort is prohibitive in lizards, using drugs to control parasite populations is extremely promising for further studies.

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