Title: **Body condition and parasite intensity correlates with escape capacity in Iberian hares *(Lepus granatensis*)**

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Summary

Preys require effective anti-predator traits to escape from predators attacks, whereas predators focus on individuals that have lower fitness. This fitness reduction is due to the effects of many regulatory forces such as parasites. We directly observed in the field the escape performance of the Iberian hare (*Lepus granatensis*) against coursing predators (measured as the time to be taken by greyhounds) and examined the relationships between parasite loads and duration of escape behaviours to test the hypothesis that predators would more easily catch substandard individuals. For some different taxa of the parasite burdens (*Taenia pisiformis* cisticercus, intestinal Coccidia) as well as for the parasite diversity, we found a negative relationship with the hare´s ability to escape. Moreover this prey´s ability is related positively to host condition. In the particular case of *T. pisiformis* cisticercus, we found a negative relationship with body condition, suggesting that its effect on anti-predation ability could be mediated by direct spoliation of host resources and/or by increasing requirements for anti-parasite defence. We approached further the question whether parasites could also induce pathology directly, affect anti-predation performance and therefore promote easier captures. Since parasite loads were not directly manipulated, experimental studies are needed in order to elucidate any causal links between parasite and anti-predatory capacity in Iberian hares.

Keywords: *Lepus granatensis*; parasites; anti-predator traits; predation; body condition

Introduction

Parasites cause constant waste on the energetic resources of most free-living organisms, by this significantly influencing their host's behaviour, demography and evolution (Holmes 1982; Minchella and Scott 1991; Sheldon and Verhulst 1996). To date, studies conducted in the wild were biased towards impacts on host fecundity and survival (e.g. Iason and Boag 1988; Murray et al. 1998; Stien 2002; Newey et al. 2004). Effects of parasites are generally viewed as reducing host fitness in an environment in which predators are not considered. However predation has the potential to magnify apparently small effects of parasites (Price et al. 1986; Ives and Murray 1997). As an example, experimental reduction of nematodes in snowshoe hare (*Lepus americanus*) did increase survival rates principally due to reduced predation on individuals with low parasites burdens (Murray et al. 1997; Murray et al. 2002). This is because parasites can make their hosts more vulnerable preys by reducing the capacity of the host-prey to avoid predators (Moore and Gotelli 1996; Vorisek et al. 1998; Joly and Messier 2004).

Predation involves complex behaviour in predator and prey interaction (Fitzgibbon 1994) which, in the case of the prey, is aimed at reducing the risk of predation and maximizing the survival probability (Caro and Fitzgibbon 1992). The variation in the effectiveness of prey defences is key to understanding the ecology and evolution of the interactions among preys and their natural enemies, which also includes parasites (Fitzgibbon 1994, Möller and Erritzöe 2000). The little available information concerning the relationships between individual host quality and susceptibility to predation in terrestrial vertebrates is systematically inferred from post-predation observations (Curio 1976; Temple 1987; Hudson et al. 1992; Murray et al. 1997). Nevertheless, it should be relatively straightforward to measure prey escape ability by direct observation (Libersat and Moore 2000). Also, by observing predatory events in the wild we can assess mechanisms that otherwise would be difficult to account for. In particular, the ability of maintaining high speed during predator attacks is an ecological relevant trait for survival (Fitzgibbon and Fanshawe 1989). A reliable testing of prey condition is mostly during coursing based predation, but less so during an ambush (Fitzgibbon and Fanshawe 1989) in which the capacity of reaction of the prey is more determinant (Murray 2002, Webster 2006).

By observing wild Iberian hares (*Lepus granatensis*) killed in coursing by greyhounds (*Canis familiaris*) in their natural habitat (Spanish plains), we aimed to test a prey selection hypothesis in which predators would more easily catch substandard individuals (Temple 1987), particularly those with higher parasite loads and in low body condition. We made three predictions: i) duration of escape is affected by prey parasite loads; ii) duration of escape is affected by body condition; and iii) reduced body condition in more parasitized individuals mediates the effects of parasites on anti-predator escape capacity (Stien et al. 2002).

Methods

The predator-prey system and direct observation of predation

The Iberian hare is a medium-sized lagomorph that inhabits the Iberian Peninsula, where a number of aerial and terrestrial predators may predate on it (Villafuerte et al. 1997). We selected Iberian greyhounds to challenge the anti-predator escape capacity of individual hares since these canids exploit their speed in open plain areas. Our direct observation of predatory events relies on a traditional and legal hare hunting system from Spanish plains. We accompanied hunters in two flat agricultural areas (managed for cereal) in the Central plateau of Spain (Ciudad Real and Toledo provinces) during 2004 and 2005 hunting seasons (from November to January). Hunting battues were carried out by 6 to 8 beaters (with two dogs each) which advanced in parallel separated by 5 m covering a band strip of terrain, causing high predator-prey encounter rates. Cereal crops, the main habitat use of the study areas, are in an early stage of growth during hunting season (late autumn, early winter) and therefore hare detection is high. Each hunter takes it in turns to pursue each flushed hare so they are pursued by two dogs. Hunters are divided in 6 teams, and we observed 187 courses; being 98 hares killed by dogs, from which we analysed a maximum of 68. Time of pursuit from hare flushing up to resolution (hunted or left) was recorded to the nearest second. We recorded the couple of dogs involved and the numbers of gathered pursuits along the hunting journey.

Laboratory analysis

By post-mortem analysis, biometry and age class (juvenile, less than 7 months, n = 20; adult, over 7 months, n = 48) of the hares were characterized (Sáenz de Buruaga et al. 1991). Individual body condition was assessed by the Kidney Fat Index (% KFI) (Iason and Boag 1988). KFI is defined as the weight of the fat that surrounds the kidney in relation to kidney weight expressed as a percentage. The respiratory and gastrointestinal tracts were removed for parasite examination and worm burden was assessed by commonly used parasitological techniques (Georgi and Georgi 1990). Organs and thoracic and abdominal cavities were inspected to quantify *Taenia pisiformis* cisticercus (Khalil et al. 1994). Coccidia oocysts of the genus *Eimeria* (Pellerdy 1974) were revealed by faecal flotation (Zinc Sulphate solution, Georgi and Georgi 1990), counted with McMaster camera and expressed as oocysts per gram of faeces.

Statistical analysis

We tested the factors affecting the length of chase and parasite scores by means of generalized linear mixed models (GLMMs, Glimmix procedure, SAS 8.01, SAS Institute). Parasite abundances were $\log_{10}$ transformed prior to analysis. Length of chase was included as continuous response variable and we separately conducted GLMMs for each parasite taxa (sample size varies slightly between analyses since all the samples were not available for every animals, Table 1) and for parasite diversity (taken as continuous explanatory variables). We also included sex (as binomial categorical), age (as binomial categorical) and body condition (assessing by KFI, % as continuous, $\log_{10}$ transformed) as explanatory variables. We controlled any accumulated tiredness in the dog due to previous physical effort by including the number of pursuits already made as explanatory continuous variables. To take into account the variation among dogs, we included the term "couple of dog" that captured the hare in a particular hunting journey as random categorical factor. These models also were fitted by locality and year as random categorical factors. We modelled with a Poisson error and a log link function (Wilson and Grenfell 1997).

We tested for the effects of parasite burdens (separately for the abundance of each taxa and for parasite diversity, as explanatory continuous variables) on body condition (% KFI, as continuous response variable, $\log_{10}$ transformed) by means of GLMMs. We also included as explanatory variables sex, age and locality (as categorical factors). The models were fitted by year as random factor, a Poisson error and an identity link function. The resulting saturated up to two interactions models were reduced by eliminating in a backward stepwise manner explanatory variables or interactions. For this purpose and to assess model fit, we used the Akaike's Information Criterion (Burnham and Anderson 1992). We used the combination probability test (Sokal and Rolf 1979) to test whether there was an overall effect of parasites on the length of chase. This test combines separate significance tests on the basis of the observed *P*-values. We used Spearman correlations to assess whether different parasites independently correlated. The level of significance was established at 5 %.

Ethical statement

The authors declare that this study is based on a legal hunting method. We were not responsible for killing the hares and did not pay for the specimens. This study has been supported by Castilla-La Mancha Government and complies with the Spanish and Castilla-La Mancha laws (Hunting Law 2/1993; RD 1095/89; RD 1118/89). This hunting method is also conformed by the Bern Convention agreements about wildlife capture and sacrifice methods (annexe VI). The hare dies immediately after the capture by one of the dogs so their suffering was limited. The hunters group we have accompanied for the experiment belongs to the Spanish Greyhound Federation (www.fedegalgos.com) who works for the improvement of the animal welfare of the two species involved in this hunting system.

Results

Hares were parasitized by intestinal adult Cestoda (Anoplocephalidae, prevalence ± SE = 16.4 ± 4.7 %, n = 61), *T. pisiformis* cisticercus (prevalence ± SE=17.6 ± 4.6 %, n=68) in thoracic and abdominal cavities, intestinal Nematoda (which included *Nematodirella* sp*., Nematodirus* sp. and *Trichostrongylus retortaeformis*, prevalence ± SE = 35.94 ± 6.0 %, n = 64) and intestinal Protozoa (*Eimeria* spp. oocysts, prevalence ± SE = 80.64 ± 5.0 %, n = 62). Mean abundances of the different parasite taxa and parasite diversity across age classes and population are shown in Table 1. No significant paired correlations were found for any parasite taxa (*P* always >0.05).

The mean length of chase when pursuit was unsuccessful was over one and half minutes (99.02 ± 6.86 sec, n = 62 timed courses). For captured individuals, the length of chase was 56.87 ± 5.63 sec for adults (n = 48) and 61.69 ± 13.58 sec for leverets (n = 20).

Concerning infection by *T. taeniformis* cisticercus, *Eimeria* spp, and parasite diversity index, we found that hares with more parasites (and those with higher parasite diversity) were captured more easily by greyhounds than hares with low parasite loads (Table 2, Figures 1 and 2). We also found that hares with a low body condition were captured more easily by greyhounds than those individuals with a high body condition (see Table 2, Figure 3). Only age differences in the length of chase was found for *T. taeniformis* cisticercus, juveniles showing slightly higher values than adults (marginal means of the model which account for the effect of parasites, were 4.11 ± 0.6 and 4.02 ±0.10 for juveniles and adults, respectively). The combination test rejected the null hypothesis that the combination of all parasite taxa did not exert an effect on the length of chase ($-2 \Sigma \ln P = 22.57$, $\chi^2 = 0.99$, d.f. = 8, $P = 0.004$).

Concerning the body condition model, *T. pisiformis* cisticercus negatively related to kidney fat index (Table 3, kidney fat indexes were 15.4 ± 0.6 % and 18.2 ± 1.3 % for infected for uninfected and uninfected hares, respectively). Adult individuals showed statistically higher body condition scores (17.02 ± 0.6 %) than juveniles (11.73 ± 0.6 %) (not significant for Coccidia, *P* value = 0.06, Table 3). Only the Cestoda model revealed that females (16.77 ± 0.7 %) showed higher body condition scores than males (13.90 ± 0.8 %).

Discussion

The main finding of this research was that anti-predator escape ability of captured hares (as direct observation revealed) and parasitism are negatively associated in Iberian hares. The general mechanism proposed for these relationships is a selection hypothesis, in which more parasitized individuals are more easily predated (Temple 1987). Only a few experimental studies have shown that parasite-induced morbidity increases vulnerability to predation: antihelminthic treatment reduced the vulnerability of snowshoe hares *Lepus americanus* (Murray et al. 1997) and red grouse *Lagopus lagopus* (Hudson et al. 1992) to predators.

We found that anti-predator escape capacity positively related to host body condition, which in turn showed a negative relationship in the particular case of *T. pisiformis* cisticercus.

This parasite taxa was negatively related to anti-predator escape capacity. Our results also suggested that these relationships were independent for each parasite.

A diversity of effects caused by parasites could be mediated by an effect on body condition (Stien 2002). Taken together, our findings suggest that the influence of *T. pisiformis* cisticercus on anti-predator escape ability could be mediated by the effect on body condition. Empirical post-hoc observations of predation support that an interaction exists between parasite-induced susceptibility to predation and the host's plane of nutrition (Curio 1976). This could be so because these parasites compete for host resources, which also need to be allocated to anti-parasite defence (Poulin 1994; Murray et al. 1997). There is increasing evidence to suggest that immuno-efficiency to control helminths is dependent upon host nutritional plane (i. e. body resources availability, Möller et al. 1998), so that it may prove to be particularly advantageous during an escape if previously engaged in this energetically demanding activity (Lauder 1991; Krist 2004). Therefore, predation of hares by greyhounds may more easily remove those individuals of the host population not only with lower body condition, but with the weakest immune response (Möller and Erritzöe 2000). We stress that we studied a subsample of the hare population composed by the individuals captured by dogs. In order to get a representative sample of the whole population, future research should include the study of hares not captured by dogs by means of an independent technique.

Parasites could also reduce escape ability causing debilitating alterations or acting by other means not directly related to any effect on body condition (as least measured as kidney fat index). This possibility illustrates importance of taking into account variation in life cycle and induced pathology of parasites with different epidemiology and life history. *T. pisiformis* cisticercus intermediate forms develop relatively large cavities in organs and tissues of hosts (usually up to 1 cm of diameter). Theses stages demand metabolic resources from the host to survive and induce a costly immune defence with large deposition of host tissue around (Anderson 2000, Maule and Marks 2006). *T. pisiformis* cisticercus are located across the thoracic and abdominal organs (Anderson 2000), and subsequently also constrains the function of affected organs and compress thoracic and abdominal muscles and bones, which should affect the running capacity of hares. Induced vulnerability to predation of moose (*Alces alces*) by wolves (*Canis lupus*) has been suggested to be caused by intermediate forms of other cestode: *Echinococcus granulosus*, hydatid cysts (Joly and Messier 2004). In this research, the main effects were attributed to lung lesions in moose, which inhibit long periods of exertion, and increase the likelihood of predation. Similarly, *T. pisiformis* cisticercus could cause respiratory distress when hares are escaping from predators.

T. pisiformis, like other parasites whose transmission relies on prey consumption by predators, would facilitate its transmission from hares to the definitive host by making the host more vulnerable to predation (Moore 2002). Evolution of this parasite-host system may have led to an efficient strategy by the parasite to ensure the continuity in this ecological community, moulding its virulence and specificity (Rigby and Jokela 2000, Pfennig 2001). A manipulative effect of parasites would only affect the behavioural trails which selectively benefit the parasite, rather than causing a general alteration of host behaviour and performance (Berdoy et al. 1995). We found for *T. taeniformis* cisticercus a negative relationship of parasite loads and body condition, a probable product of competitive relationships in the host. Therefore, our finding suggests that any effect of *T. taeniformis* infection would be general rather than specific.

Sublethal effects of intestinal parasites usually work through diminishing the metabolic efficiency of the organism and availability of resources by damaging enteric mucosa and reducing nutrient absorption during the digestion process (e. g. Watson et al., 1987). Subsequently, intestinal parasites could have an indirect effect on locomotory function by causing a reduction in available resources. At high infection rates they are able to cause a more severe pathology, like host blood draining with subsequent body systemic affectation and decline in locomotory performance (Gulland 1992). We did not find evidence for a relationship between intestinal parasite loads and condition. Nevertheless intestinal parasites, even at low infection intensities may affect the general locomotion function by decreasing the performance of the neuromuscular system (at the level of neuronal mediators, see Kavaliers and Colwell 1994).

In summary, the characterization of predation events on naturally infected hares proved to be an advance in terms of studying how natural enemies of host preys interact. Our phenotypic correlational approach supports the idea that escape capacity against predation in the wild is a relevant and sensitive measure of prey biological efficiency. We conclude that including the study of behavioural aspects in hares not captured by dogs should clarify whether parasites influence anti-predation behaviours by reducing the risk of predation and maximizing the survival probability.

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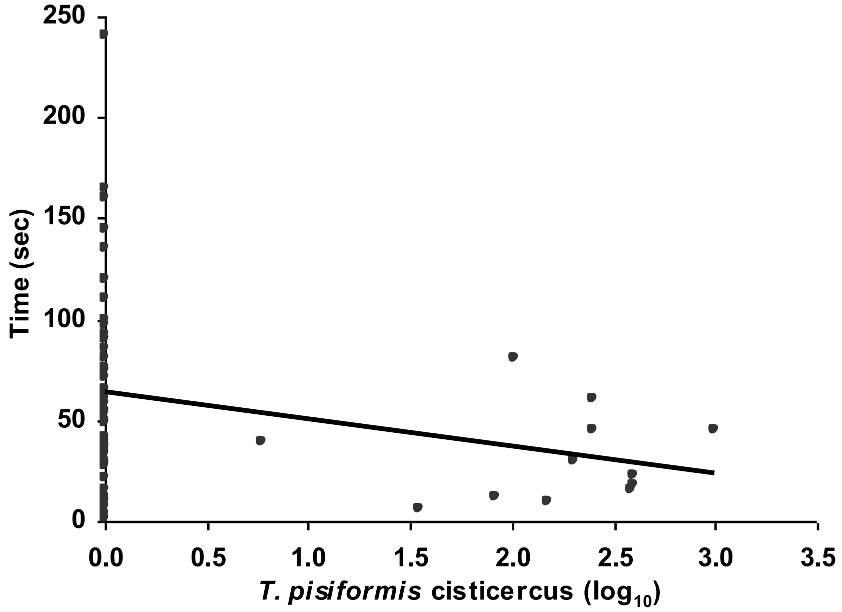
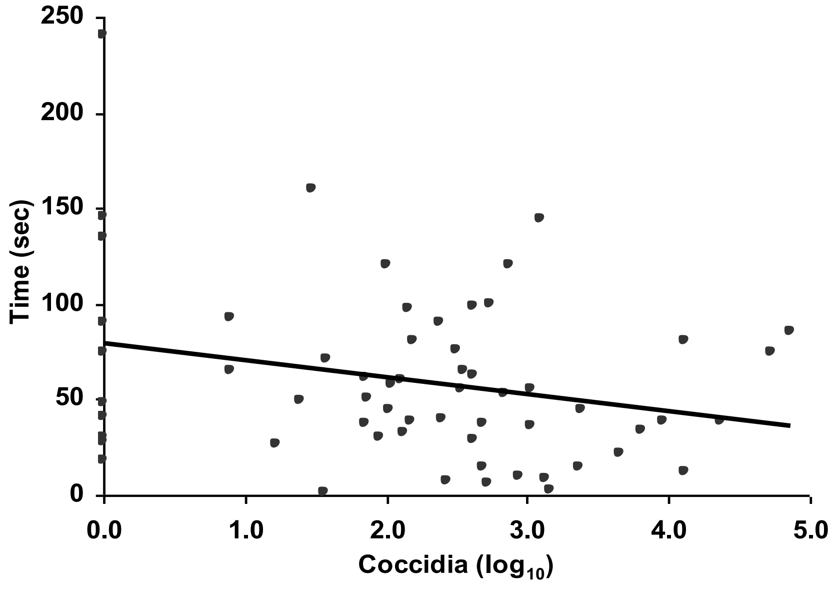
Figure 1.

(a)



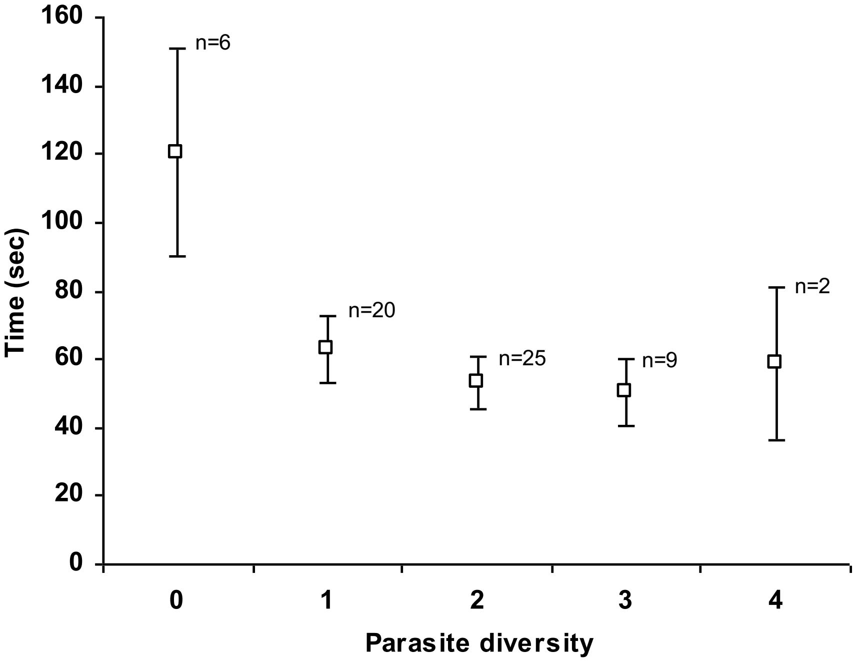
250
200
150
100
50
0
Time (sec)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
T. pisiformis cisticercus (log10)

(b)



250
200
150
100
50
0
Time (sec)
0.0
1.0
2.0
3.0
4.0
5.0
Coccidia (log10)

Figure 2.



160
140
120
100
80
60
40
20
0
Time (sec)
n=6
n=20
n=25
n=9
n=2
0
1
2
3
4
Parasite diversity

Figure 3.

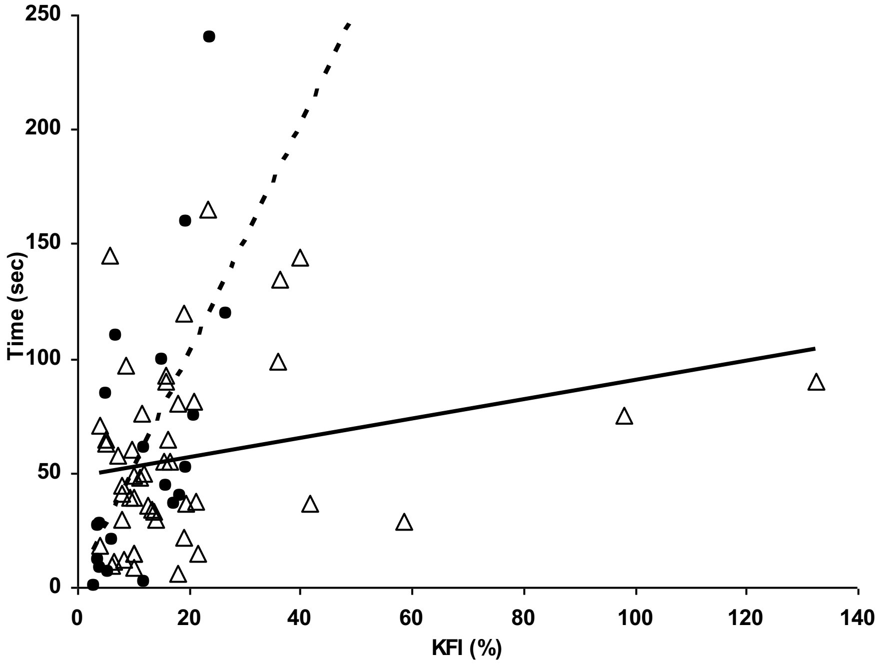


Table 1. Parasite abundances (mean abundance, standard error and sampling size) of the difference parasite taxa, and parasite diversity index (PDI) across age classes (a) and sampling sites (b).

(a)	**Leverets**			**Adults**		
	Mean	**SE**	**n**	**Mean**	**SE**	**n**
T. pisiformis	12.5	12.5	20	62.6	25.1	48
Nematoda	0.2	0.1	18	9.3	3.1	46
Cestoda	0.1	0.1	18	0.2	0.1	43
Coccidia	4914.2	4490.9	16	3130.2	1364.8	44
PDI	1.2	0.2	16	1.9	0.1	46
(b)	**Ciudad Real**			**Toledo**		
	Mean	**SE**	**n**	**Mean**	**SE**	**n**
T. pisiformis	66.3	24.9	49	0.3	0.3	19
Nematoda	2.0	1.3	45	18.0	6.1	19
Cestoda	0.2	0.1	42	0.1	0.1	19
Coccidia	4842.1	2214.8	41	938.5	683.3	19
PDI	1.5	0.1	41	2.3	0.2	21

Table 2. Test statistics of GLMM for effects of different abundances and diversity (PDI) of parasites (grouped according to first row) on chase time (dependent variable, sec). Parameter estimates (E) for the level of fixed factor were calculated considering a reference value of zero for female level in the variable “Sex” and adult level in the variable “Age”. All the models were fitted by locality (Ciudad Real/Toledo, $P > 0.05$ in every model) hunting season (2004/2005, $P > 0.05$ in every model) and involved predators ($P > 0.05$ in every model, except by “Coccidia” model, $P = 0.03$). ([a]) Explained deviance and ([b]) scaled deviance. Degree of freedom refers to the maximum value in the model. Only the significant factors values are represented.

Parasite ►	*T. pisiformis* (df=59)			Nematoda (df=51)			Cestoda (df=48)			Coccidia (df=49)			Parasite diversity (df =46)		
Variable▼	*F*	*P*	E	*F*	*P*	E	*F*	*P*	E	*F*	*P*	E	*F*	*P*	E
Age	5.93	**0.02**	-1.78	-	-	-	-	-	-	-	-	-	-	-	-
KFI	18.48	**<0.01**	0.44	11.19	**<0.01**	0.47	12.69	**<0.01**	0.52	14.12	**<0.01**	0.75	11.79	**<0.01**	0.49
Parasite (or PDI)	4.39	**0.04**	-0.25	1.69	0.19	0.04	1.01	0.33	-2.18	7.73	**<0.01**	-0.17	7.28	**0.01**	-0.23
Sex*age	-	-	-	2.43	0.08	-	2.77	0.06	-	5.36	**<0.01**	-	4.86	**<0.01**	-
Age*KFI	7.78	**<0.01**	1.71	2.56	0.11	1.24	2.61	0.11	1.10	2.75	0.11	1.08	3.82	0.06	1.28
Ex. dev.[a], Sc. dev.[b]	50.05 %, 51.74			66.39 %, 37.52			62.64 %, 34.89			75.88 %, 31.23			55.12 %, 41.41		

Table 3. Test statistics of GLMM for effects of different abundances and diversity (PDI) of parasites (grouped according to first row) on body condition (kidney fat index as dependent variable, %). Parameter estimates (E) for the level of fixed factor were calculated considering a reference value of zero for female level in the variable "Sex" and adult level in the variable "Age". As random factors, all the models were fitted by locality (Ciudad Real/Toledo, $P > 0.05$ in every model) and hunting season (2004-2005, $P > 0.05$ in every model). ([a]) Explained deviance and ([b]) scaled deviance. Degree of freedom refers to the maximum value in the model. Only significant terms (at least in a model) are shown.

Parasite ►	*T. pisiformis* (df=69)			Nematoda (df=64)			Cestoda (df=61)			Coccidia (df=57)			Parasite diversity (df =57)		
Variable▼	*F*	*P*	E	*F*	*P*	E	*F*	*P*	E	*F*	*P*	E	*F*	*P*	E
Age	**8.70**	**<0.01**	**-0.40**	**6.37**	**0.01**	**-0.4**	**6.81**	**0.01**	**-0.40**	3.43	0.06	-0.30	**4.15**	**0.04**	**-0.33**
Parasite (or PDI)	**4.83**	**0.03**	**-0.1**	2.56	0.11	0.04	0.02	0.88	0.03	0.34	0.56	0.01	0.51	0.48	-0.03
Sex*age	3.78	0.05	-	**5.44**	**0.02**	**-**	3.70	0.06	**-**	1.92	0.17	-	1.83	0.18	-
Leveret*male	-	-	0.28	-	-	0.37	-	-	0.32	-	-	0.25	-	-	0.24
Ex. dev.[a], Sc. dev.[b]	15.40 %, 5.78			13.95 %, 5.35			12.26 %, 5.37			16.18 %, 4.76			8.42 %, 5.19		

Figure legends

Figure 1. Abundance of *Taenia pisiformis* cisticercus (a) and intestinal Coccidia (b) parasitizing hares plotted against the length of chase (sec) recorded for the respective host (n = 68, and n = 60; respectively). It should be noted that in this regression scatter plot the partial effects of the other explanatory variables upon the dependent ones are not accounted for.

Figure 2. Relationships between the parasite diversity index and mean values for length of chase (sec). It should be noted that in graph the partial effects of the other explanatory variables upon the dependent ones are not accounted for.

Figure 3. Relationship between body condition (Kidney Fat Index, %) and length of chase (sec) across leverets (n = 20) and adult hares (n = 48); respectively. It should be noted that in this regression scatter plot the partial effects of the other explanatory variables upon the dependent ones are not accounted for. (•) refers to leverets, Δ refers to adults, (-----) is the lineal regression line for leverets, (——) is the lineal regression line for adults.