



RESEARCH PAPER

Complex Relationships amongst Parasite Load and Escape Behaviour in an Insular Lizard

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Abstract

Economic escape models predict escape decisions of prey which are approached by predators. Flight initiation distance (FID, predator–prey distance when prey begins to flee) and distance fled (DF) are major variables used to characterize escape responses. In optimal escape theory, FID increases as cost of not fleeing also increases. Moreover, FID decreases as cost of fleeing increases, due to lost opportunities to perform activities that may increase fitness. Finally, FID further increases as the prey's fitness increases. Some factors, including parasitism, may affect more than one of these predictors of FID. Initially, parasitized prey may have lower fitness as well as impaired locomotor ability, which would avoid predation and/or reduce their foraging ability, further decreasing the opportunity of fleeing. For example, if parasites decrease body condition, prey fitness is reduced and escape ability may be impaired. Hence, the overall influence of parasitism on FID is difficult to predict. We examined relationships between escape decisions and different traits: parasite load, body size and body condition in the Balearic lizard, *Podarcis lilfordi*. Lizards that showed higher haemogregarines load had longer FID and shorter DF. Although results did not confirm our initial predictions made on the basis of optimal escape theory, our findings suggest that parasites can alter several aspects of escape behaviour in a complex way.

Introduction

The recognition and avoidance of predators are essential for animals because a mistake or lack to do may lead to death. Therefore, there is a strong selection on escape behaviour. The variables currently used to assess escape decisions made by prey are flight initiation distance (FID), the distance separating an approaching predator from prey when escape begins, and distance fled (DF), which refers to the total distance covered during active flight. These variables are important indicators of assessed risk of not fleeing and cost of fleeing. According to optimal escape theory (Cooper & Frederick 2007, 2010), escape decisions are based on three aspects: effects of predation risk, cost of escaping and current fitness.

By including prey's initial fitness, we incorporate Clark's asset protection principle (1994), which states that individuals that have greater residual reproductive value should be more risk-averse (Poulin 1993; Clark 1994; Poulin et al. 1994; Roff 2002). In the context of escape, prey with higher initial fitness should have longer FID to protect their expected lifetime fitness.

Parasitism has multiple potential effects on escape decisions (Cooper & Frederick 2010). Parasites affect host fecundity (Schall 1983; Møller 1993), reproductive success (Schall 1996; Oppliger et al. 1997) and sexual selection of hosts (Hamilton & Zuk 1982; Møller et al. 1999). It is even an important cause of mortality (Schall 1983, 1996; but see Eisen 2001), reducing life expectancy (e.g. Sorci & Clobert 1995;

Møller 1997) and residual reproductive value of hosts. Hence, for most parasitized organisms, lower initial fitness should favour decreased FID (Clark 1994; Cooper & Frederick 2010).

Parasitism may have another major effect: the reduction of escape ability, which counteracts initial fitness. Several studies have shown that most parasitized hosts experience a disproportionately larger predation risk (Møller & Nielsen 2007; Genovart et al. 2010). In addition, impaired metabolic efficiency and locomotor performance of infected organisms reduce escape ability (Shine 1980; Bauwens & Thoen 1981; Schall et al. 1982). In lizards, sprint speed decreases as loads of blood parasite (Oppliger et al. 1996; Garrido & Pérez-Mellado 2014 for the same population) and ectoparasite increase (Main & Bull 2000; see, however, Garrido & Pérez-Mellado 2014). As a result, escape ability of the most parasitized individuals is reduced, and their own perception of risk is predicted to be greater, unless the parasites also affect cognitive processes related to predator detection or escape. Consequently, if risk assessment is unimpaired, the effects of parasitism on escape ability are predicted to result in longer FID and shorter DF.

This study examines the effects of parasitism on escape behaviour in an insular population of *Podarcis lilfordi* lizard. This population shows high rates of infection by blood-borne microparasites (haemogregarines) and macroparasites (mites) (Garrido & Pérez-Mellado 2013a,b). On the one hand, FID may be shorter if the effect of lower fitness is stronger than the effect of lower speed, and on the other hand, it may be longer if, due to lower speed, greater predation risk predominates (Cooper & Frederick 2010). Moreover, individuals in better physical condition (i.e. lizards with intact tails or higher fat store) perform longer FIDs (review in Stankowich & Blumstein 2005), which is consistent with a predominant effect of initial fitness. Therefore, asset protection appears to have outweighed the greater risk associated with reduced running speed in these cases. These findings suggest that low body condition may have a stronger effect on FID via the reduction of initial fitness than via a risk imposed by the reduction of running speed. Thus, we expect highly parasitized lizards to perform shorter FIDs and, as escape ability is reduced, resulting in shorter DFs. Nevertheless, the overall effect of parasitism on FID is difficult to predict; the multiple interactions of diverse effects caused by parasites may lead to failure of predictions based solely on single factors (Cooper & Frederick 2010).

Methods

Study Species and Site

Podarcis lilfordi (Squamata, Lacertidae) is a medium-sized lacertid lizard endemic to the Balearic Islands (Pérez-Mellado 1998). The field work was done on two warm sunny days of Jun. 2011, on Aire Island (Balearic Islands, Spain; 39°48'N, 4°17'E, 15 m.a.s.l.). Aire Island has a surface of 34 ha and is about one mile from the south-eastern coast of Menorca. The vegetation is highly influenced by its environmental characteristics (strong winds, high salinity and long drought periods) and dominated by low shrubs and a variety of herbaceous plant species. Lizard densities can be very high, with over 4000 individuals per hectare (Pérez-Mellado et al. 2008).

No mammalian or ophidian predators of lizards are present on Aire (Pérez-Mellado 1989); instead, birds are the main predators. Kestrels (*Falco tinnunculus*) do not breed on Aire, but visit the islet frequently and are the major predators of *P. lilfordi*. Breeding colonies of two gull species (*Larus michahellis* and *Ichthyophaga audouinii*), which very occasionally capture lizards, are present on Aire (Pérez-Mellado et al. 2014; see also Martín & López 1990; Martínez-Abraín et al. 2003; Matias & Catry 2010).

Experimental Procedure

Escape behaviour trials were conducted from 0700 to 1200 h GMT when lizards were fully active. To study escape responses, we acted as simulated predators. Humans have been very useful as simulated predators in escape experiments with different taxa (reviewed by Stankowich & Blumstein 2005). In some previous studies on Aire population, lizards reacted to researchers in response to natural predators as was expected (Cooper et al. 2009a; Pérez-Cembranos et al. 2013). In the current study, the experimental procedure is similar to the one used in those previous studies. Before trials, the researcher slowly walked through the area searching for an active lizard. After detecting one of them, he moved to a location that allowed the lizard to view the researcher at a starting distance of 5–10 m. All individuals were tested on the ground or rocks. In previous experiments on the same population, we did not detect any significant effect of the microhabitat in escape responses (e.g. Cooper et al. 2009b,c). In all trials, the same experimenter approached the lizard directly at a practiced speed of 80 m/min. At this speed, starting distance has no effect on FID in *P. lilfordi* (Cooper et al. 2009a). As

soon as the lizard fled, the researcher stopped and recorded FID and DF by the lizard before stopping for at least 1 s. *P. lilfordi* sometimes hide in a refuge when they escape, but they generally remain in sight after fleeing (Pérez-Cembranos et al. 2013). When we finished the trial for one individual, another individual was usually in sight, the researcher moved again to a location that allowed the lizard a clear view of him, always keeping a starting distance of 5–10 m. Because escape behaviour often differs amongst age and sex groups (Stankowich & Blumstein 2005), we tested only adult males. After each trial, the lizard was captured by noosing. Capture rate was very high, and it was only very few individuals which were discarded from the analysis, as we were not able to capture them. To ensure that each individual was studied only once, captured lizards were marked with colour pens.

For each of the 30 individuals, we recorded the following traits: body size (measured as snout-vent length), tail length, hindlimb length and body mass (Table 1). At the site of capture, we counted ectoparasites using a 5× monocle (Eschenbach) to inspect the whole body surface. To obtain blood samples, we made a tiny lengthwise cut (<5 mm in all cases) on the dorsal side of the tail with a sterile scalpel. Garrido & Pérez-Mellado (2013a) observed the cut in the tail of previously studied individuals two or three seasons later and confirmed that this technique did not impair lizards. We smeared *in situ* a drop of blood on a slide that we dried in the field. After blood sampling, lizards were released at the site of capture. In the laboratory, slides were fixed with absolute methanol for 10 min and then stained with modified Giemsa for 20 min.

Table 1: Descriptive statistics of the variables employed to describe relationships amongst parasite load and escape behaviour in the insular lizard *Podarcis lilfordi* (n = sample size, se: standard error)

	n	$\bar{x} \pm SE$	Minimum	Maximum	Range
Body mass (g)	30	10.83 \pm 0.34	7.5	15.5	8
Body size (mm)	30	72.02 \pm 0.65	64.5	78.5	14
Hindlimb length (mm)	30	36.82 \pm 0.31	34.38	39.66	5.28
Haemogregarine load (infected cells/2000 red blood cells)	30	21.73 \pm 3.87	0	89	89
Mite load	30	72.62 \pm 11.18	0	245	245
Body condition	30	0.28 \pm 0.17	-0.9	2.48	3.38
Flight initiation distance (FID) (cm)	30	138.77 \pm 9.82	66	290	224
Distance fled (DF) (cm)	30	80.53 \pm 5.91	40	150	110

Samples were analysed using an optical microscope (Carl Zeiss KF2) at 400×. Much as in previous studies, the only blood parasites identified in the present study were haemogregarines (Garrido & Pérez-Mellado 2013a,b). Haemogregarines were assigned to the genus *Hepatozoon* (A. Marzal, unpubl. data and pers. comm.). All ectoparasites found were assigned to Trombiculidae family (larvae of chigger mites, M. Moraza, pers. comm.). The intensity of parasitism by haemogregarines was estimated by counting the number of parasites observed per 2000 red blood cells (Table 1). Prevalence of infestation, estimated as the percentage of individuals infected with haemogregarines and ectoparasites, was 96.7% and 90.0%, respectively (29/30 and 27/30 individuals). These results are consistent with those found for *P. lilfordi* adult males in previous studies at the same location (Garrido & Pérez-Mellado 2013a,b, 2014). To estimate body condition and relative hindlimb length, we used un-standardized residuals from linear regressions of log-transformed body mass and hindlimb length on log-transformed body size, respectively.

Statistical Analysis

The statistical analyses were performed in R environment (ver. 2.12.1; R Development Core Team 2010). We carried out a multiple linear regression analysis (Quinn & Keough 2002) to determine which variables were more related to FID and DF. The analysed variables included haemogregarine load, mite load and body condition. We also included the relative hindlimb length and body size (measured as snout-vent length) as they could influence FID and DF (Bauwens et al. 1995; Cooper 2011). Homogeneity of variance was examined using Fligner tests, and normality was assessed using Shapiro–Wilk's tests. Both haemogregarine and mite load values were square-root transformed to obtain normality. For the same purpose, FID and DF were log-transformed. We tested for collinearity of the explanatory variables; any variable with a variance inflation factor (VIF) >3 should be discarded (Zuur et al. 2010). In this study, all variables had values lower than this threshold value (VIF: haemogregarine load = 1.12; mite load = 1.09; body condition = 1.17; relative hindlimb length = 1.11; body size = 1.04). Therefore, no correlation was found between variables, and all of them were included in the model (see below). As shown in previous studies, ecological relationships between parasitism and body condition are complex in Aire Island, and we did not obtain any evidence to support a significant correlation between the above-mentioned

variables in the population under study (Garrido & Pérez-Mellado 2013a,b, 2014).

With five predictor variables, a linear model with all possible interactions would have 32 model terms. This model would be extremely difficult to interpret (Quinn & Keough 2002). In light of this, we fitted an additive model considering the effects of all independent variables and using a forward selection; we then added the variables with greatest F statistic (Quinn & Keough 2002). Then, we fitted a multiplicative model including interaction terms of the variables retained in the additive model. To select the best model, we considered at each step the larger value of adjusted r^2 along with the minimal value of the Akaike's Information Criterion (AIC) and the Bayesian Information Criterion (BIC, Quinn & Keough 2002). Effect sizes were reported for significant continuous predictors included in the final model as partial correlation coefficients (r) (Nakagawa & Cuthill 2007). Prior to the model, we analysed the potential influence of the time of day and hourly interval on escape behaviour of lizards.

Results

Effect of Time of Day

Neither the time of day (Fligner test: $\chi^2 = 28.94$, d.f. = 27, $p = 0.36$; GLM, $F_{1,28} = 1.79$, $p = 0.19$) nor the hourly interval ($\chi^2 = 6.10$, df = 4, $p = 0.19$; GLM, $F_{4,25} = 0.84$, $p = 0.51$) was significantly related to FID. Results were similar for DF. Neither the time of day (Fligner test: $\chi^2 = 28.71$, df = 27, $p = 0.38$; GLM, $F_{1,28} = 0.47$, $p = 0.50$) nor the hourly interval (Fligner test: $\chi^2 = 2.17$, df = 4, $p = 0.71$; GLM, $F_{4,25} = 1.15$, $p = 0.36$) was significantly related to DF.

Effects of Parasites on FID

Flight initiation distance increased as haemogregarines load increased, but mite load and body condition did not show an effect (Fig. 1). Following forward selection procedure, we started with a null model and introduced, at each step, the predictor with highest value of partial F statistic (Quinn & Keough 2002). Hence, we first added haemogregarine load, followed by body condition and, finally, mite load (Table 2). Up to this point, having included each predictor in the model, AIC and BIC values decreased and the value of adjusted r^2 increased. With the inclusion of relative hindlimb length, AIC and BIC values were slightly reduced, but the value of adjusted r^2 decreased strongly (Table 2). With the inclusion of body size,

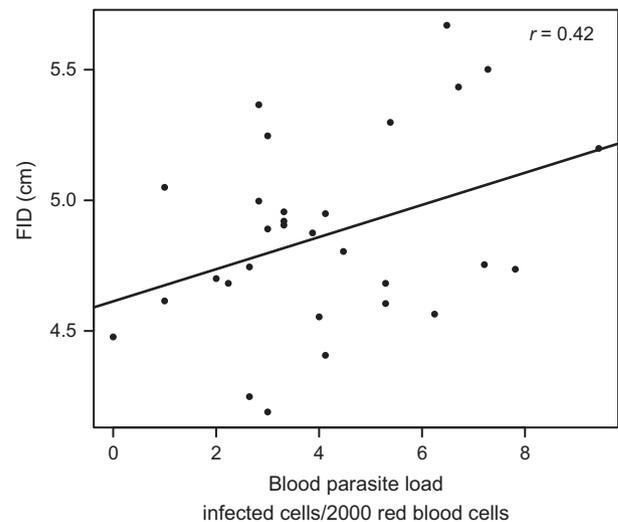


Fig. 1: Relationship between flight initiation distance (FID) and haemogregarine load (data were square-root transformed to reach normality assumption) in the Balearic lizard, *Podarcis lilfordi*.

Table 2: Forward selection procedure to fit the best flight initiation distance (FID) model. Inclusion of predictors in the model (from up to down) at each step was done according to highest value of partial F statistic. To select the best model, we considered at each step the larger value of adjusted r^2 along with the minimal value of the Akaike's Information Criterion (AIC) and the Bayesian Information Criterion (BIC, Quinn & Keough 2002)

	F	r^2	AIC	BIC
Null model			27.14	29.94
Haemogregarine load	4.56	0.11	24.61	28.82
Body condition	2.71	0.16	23.74	29.34
Mite load^a	1.66	0.17	24.62	31.45
Body size	0.27	0.14	26.57	34.78
Relative hindlimb length	0.78	0.016	17.63	24.18
Interaction terms				
Haemogregarine load	0.04	0.15	28.09	40.40
*Body condition*Mite load				
Body condition*Mite load	3.08	0.23	23.11	31.31

Variables finally included in the model were in bold.

^aFollowing Quinn & Keough 2002, despite slightly increased AIC and BIC, mite load was included in the final model as increased r^2 and their interaction with body condition strongly improve the model.

AIC, BIC and adjusted r^2 showed worse values (Table 2), so we decided to exclude both relative hindlimb length and body size from the additive model.

The multiplicative model, including all possible interactions between previously introduced variables (mite and haemogregarine load and body condition), also showed worse values for the three estimators (Table 2), and as a consequence, this model was

discarded (Quinn & Keough 2002). Only the inclusion of the interaction between mite load and body condition improved the additive model (Table 2). The remaining interactions showed a p value above 0.66 (all $F < 0.19$). The minimal adequate model for FID ($F_{4,24} = 3.13$, $p = 0.03$; Table 3) revealed that haemogregarine load was significantly linked to FID, showing a medium-size effect. Mite load, body condition and their interaction term were retained in the model but were not significantly related with FID despite their effect size (Table 3).

Effects of Parasites on DF

Distance fled increased as body size increased, but decreased as haemogregarine load increased (Fig. 2). Following the same procedure and starting from null

model, haemogregarine load was the first variable included in DF model, followed by body size (Table 4). The inclusion of the remaining factors, relative hindlimb length, mite load and body condition (Table 4), worsened the model as the estimators shown.

The inclusion of the interaction term between haemogregarine load and body size improved the model (Table 4). Hence, the best model for DF ($F_{3,26} = 5.15$, $p < 0.01$; Table 3) included only body size, haemogregarine load and their interaction term (Table 5), although this term is not significant. The three predictors showed a medium-size effect, being larger for body size (Table 5).

Discussion

Results partially confirmed our initial predictions: highly parasitized lizards performed shorter FIDs as

Table 3: Results of the multiple regression (minimal adequate model) for flight initiation distance (FID) in adult males of *Podarcis lilfordi* on Aire Island (Menorca, Spain). FID was log10 transformed, and haemogregarine and mite load values were square-root transformed to reach normality assumption. Effect size was reported as partial correlation coefficients (r , see Nakagawa & Cuthill 2007)

	df	Sum sq	\bar{x}^2	F	Pr(>F)	Slope	r
Haemogregarines	1	0.54	0.54	5.24	0.031*	0.07	0.42
Body condition	1	0.38	0.38	3.67	0.068	0.28	0.24
Mites	1	0.06	0.06	0.53	0.472	-0.02	0.23
Mites:condition	1	0.32	0.32	3.09	0.092	-0.04	0.34
Residuals	24	2.49	0.10				

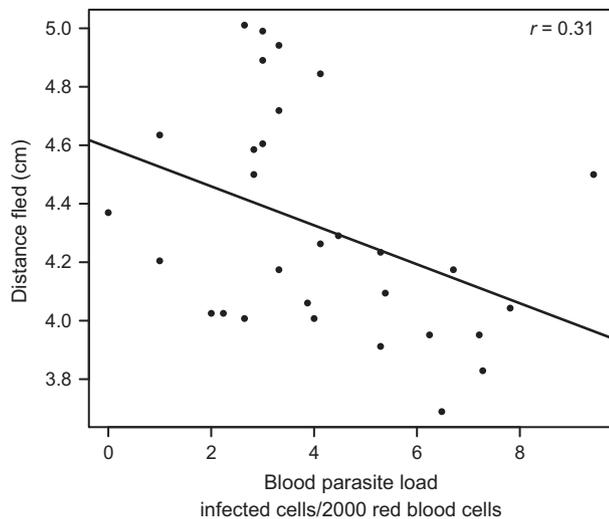


Fig. 2: Relationship between distance fled (DF) and haemogregarine load (data were square-root transformed to reach normality assumption) in the Balearic lizard, *Podarcis lilfordi*.

Table 4: Forward selection procedure to fit the best distance fled (DF) model. Inclusion of predictors in the model (from up to down) at each step was done according to highest value of partial F statistic. To select the best model, we considered at each step the larger value of adjusted r^2 along with the minimal value of the Akaike's Information Criterion (AIC) and the Bayesian Information Criterion (BIC, Quinn & Keough 2002)

	F	r^2	AIC	BIC
Null model			29.42	32.22
Haemogregarine load	5.03	0.12	24.46	30.67
Body condition	0.04	0.09	28.42	34.03
Mite load	0.78	0.11	24.94	30.41
Body size	4.56	0.25	22.77	28.38
Relative hindlimb length ^a	2.11	0.06	19.85	24.39
Interaction terms				
Haemogregarine load*Body size	3.07	0.30	21.43	28.44

Variables finally included in the model were in bold.

^aFollowing Quinn & Keough 2002, despite decreased AIC and BIC, relative hindlimb length was not included in the final model as drastically decreased r^2 .

Table 5: Results of the multiple regression (minimal adequate model) for distance fled (DF) in adult males of *Podarcis lilfordi* on Aire Island (Menorca, Spain). Flight initiation distance was log10 transformed, and haemogregarine and mite load values were square-root transformed to reach normality assumption. Effect size was reported as partial correlation coefficients (r , see Nakagawa & Cuthill 2007)

	df	Sum sq	\bar{x}^2	F	Pr(>F)	Slope	r
Haemogregarines	1	0.62	0.62	6.31	0.02*	1.09	0.31
Body size	1	0.60	0.60	6.07	0.02*	0.11	0.45
Haemogregarines: Body size	1	0.30	0.30	3.07	0.09	-0.02	0.37
Residuals	26	2.57	0.10				

well as shorter DFs because escape ability was reduced. Amongst parasites, only haemogregarines affected FID and DF in *P. lilfordi*, but it did so in opposite ways: FID increased as haemogregarine load increased, but DF decreased as haemogregarine load increased. As was explained in the Introduction, optimal escape theory (Cooper & Frederick 2007, 2010) predicts that FID increases as risk of predation assessed by the prey increases, it decreases as cost of fleeing increases, and it further increases as the prey's fitness (residual reproductive value) increases. The increase in FID as haemogregarine load increased was consistent with a greater perceived predation risk, a minor opportunity cost of fleeing or greater prey's initial fitness at higher parasite loads. Because sprint speed decreases as haemogregarine load increases (Garrido & Pérez-Mellado 2014), predation risk at a given predator-prey distance increases with load. Then, as was previously observed and as escape theory predicts, FID increased with haemogregarine load.

Effects of the haemogregarines on costs of fleeing (or not) might be dictated by decrease of running speed or other aspects of escape ability, but also by lower feeding rates amongst heavily parasitized individuals. However, under some circumstances, larger and more heavily infected *P. lilfordi* males are better able to obtain food associated with available resources (Garrido & Pérez-Mellado 2013a), which would lower the cost of missing a feeding opportunity when they flee. In this case, the increase in FID with haemogregarine load might be attributable to the greater initial fitness and reduced sprint speed of large males which have high haemogregarine loads, but not to greater cost of fleeing. Nevertheless, we have no evidence that the studied lizards were better able to obtain food at any time.

Haemogregarine infections can be fatal in laboratory conditions (Schall 1996), but the effects of lower loads and of the haemogregarines species observed in our study on mortality and health are unknown. Be that as it may, assuming that fitness is reduced with parasite load, the effects of the greater initial fitness and greater assessed predation risk appear to have outweighed alleged reduction in fitness. We suggest that the haemogregarine loads which prevail in our population of lizards having a limited, but adequate, food supply and exposed to low levels of predation (Pérez-Mellado & Corti 1993; Cooper & Pérez-Mellado 2012) do not reduce fitness substantially. The fact that body condition was unrelated to either FID or DF in relation to haemogregarine load further suggests that haemogregarines may not greatly affect fitness in the studied population, as previous studies suggest

(Garrido & Pérez-Mellado 2013a,b, 2014). Alternatively, enhanced thermoregulatory and feeding opportunities of large males might counteract any negative effect of the parasites.

The lack of effect of body condition on FID occurred despite slower sprint speed of lizards in worse body condition (Garrido & Pérez-Mellado 2014). Large males have high initial fitness and may have high haemogregarine loads acquired via high activity, aggressive behaviour and possibly enhanced by immunosuppression due to aggression that causes greater susceptibility to infection (Garrido & Pérez-Mellado 2013a). These findings suggest that the high initial fitness of large males, which is not to say greater predation risk, is the primary factor responsible for the increase in FID as haemogregarine load increases.

Haemogregarine load also affected the DF, which decreased as parasite load increased, according to our predictions. Nonetheless, our results were the opposite of the increase in DF predicted by escape theory for effects of predation risk and initial fitness. Effects of reduced escape ability of highly parasitized lizards (Garrido & Pérez-Mellado 2014) predominated. Causes of variation for DF are less well understood than for FID. DF may vary amongst age/size groups (Stankowich & Blumstein 2005) and is strongly affected by distance to refuge in some prey (Stankowich & Blumstein 2005). Consistent with previous findings (Cooper et al. 1990), heavily parasitized individuals may show greater reliance on refuge and flee inside or near refuges before stopping. This is unlikely because, although *P. lilfordi* sometimes use refuges, they generally remain in sight after fleeing. It is also possible that factors which affect the decision to begin fleeing and how far to flee are affected differently by haemogregarines or other associated ecological or behavioural factors. Parasites can drastically alter host behaviour, including antipredatory behaviour (e.g. Moore 2002; Liebersat et al. 2009; e.g. rabies).

To our knowledge, this is the first study to report a positive correlation between FID and parasite load, in this case for haemogregarines of individual lizards. Several studies have shown that FID can be affected by tail autotomy positively, negatively or not at all (Stankowich & Blumstein 2005; Cooper 2007; Cooper & Wilson 2008). In the lizard, *Sceloporus virgatus* running speed is reduced (Cooper et al. 2009d), and FID is increased following tail loss (Cooper 2007; Cooper & Wilson 2008). The lack of correlation between FID or DF and mite load could be expected. In previous studies in lizards, individuals infected by blood parasites, but not ectoparasites, tended to have reduced

escape ability due to lowered metabolic efficiency (Atkinson & Van Riper 1991; Chen et al. 2001). Blood-borne parasites have more harmful effects on the physiology of hosts than mites or ticks (Schall et al. 1982; Oppliger et al. 1996; Garrido & Pérez-Mellado 2013b and references therein).

The lack of relationship between body size and FID as well as the positive correlation between body size and DF in *P. lilfordi* is unique. The increase in DF as body size increases might simply indicate that larger lizards run farther while expending equal effort to flee. However, this seems unlikely as body size is not related to speed in adult males from Aire Island (Garrido & Pérez-Mellado 2014). Alternatively, larger individuals that represent a greater energetic benefit to predators might be at greater risk of being pursued or more likely to be pursued more vigorously once they begin to flee. Larger adults might also be farther from effective refuges. In previous lizard studies, FID increased with body size in ten species (Shallenberger 1970; Martín & López 1995, 2003; Whiting et al. 2003; Carretero et al. 2006; Brecko et al. 2008; Cooper 2011) and decreased from hatchlings to adults in another species (Berger et al. 2007). Because all of these studies included hatchlings and/or juveniles as well as adults, the range of body size amongst adult males in our study was likely to have been too small to reveal any covariation of body size and FID. The relationships between body size and DF were variable: DF increased with body size in one species (Martín & López 1995), decreased in another (Whiting et al. 2003) and was unrelated to body size in two others (Martín & López 2003). The increase in DF as body size increases in adult male *P. lilfordi* agrees with the relationship found in a study of another lacertid species in which the entire size range from hatchlings to adults was examined (Martín & López 1995).

Because our study was correlational rather than experimental, the relationships detected do not necessarily indicate that haemogregarines caused modification of escape decisions; other ecological and behavioural factors could influence both FID and parasite load. In the absence of other influences and according to Clark's principle, FID is expected to increase with body condition increasing. Males that aggressively defend resources from conspecifics have high body condition and are more exposed to male-male aggressive encounters (Garrido & Pérez-Mellado 2013a). In male-male interactions, lizards commonly bite each other's tail and even caudal autotomy and tail consumption by the opponent may occur (Garrido & Pérez-Mellado 2013a). Therefore, the ingestion of mites in the tail may increase the probability of

transmission of parasites between males (Smith 1996; Telford 2008; Lledó et al. 2010; Garrido & Pérez-Mellado 2013a). In addition, larger males are more exposed to stressful conditions, due to aggression and competition for resource, which may enhance immunosuppression and affect disease resistance (Oppliger et al. 1998; Garrido & Pérez-Mellado 2013a). Therefore, aggression and high activity can account for the higher load of blood-borne parasites amongst males in good body condition. Thus, males with high parasite loads presumably have longer FID because they are protecting the asset (Clark 1994) of higher fitness associated with good condition.

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