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Sprint speed is related to blood parasites, but not to ectoparasites, in an insular population of lacertid lizards

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Abstract: Parasites are able to negatively affect the locomotor performance of their hosts, and consequently, their biological fitness. In this study, we examine the relationship between parasitism and burst speed in an insular population of Lilford's Wall Lizard (*Podarcis lilfordi* (Günther, 1874)). *Podarcis lilfordi* is normally infected with haemogregarine blood parasites and mites in our study location, Aire Island (Balearic Islands, Spain). Unlike the results from other studies on lizards, we found a significant negative correlation between intensity of infection by haemogregarines and burst speed. Body condition is also significantly related to burst speed. Thus, lizards with a lower blood parasite load and better body condition show a faster sprint speed. Intensity of infection by haemoparasites shows a lack of correlation with both body condition and mite load. Our results are compared with those from other lizard species living in different habitats. We discuss the influence of insular environmental conditions on locomotor performances, such as low predation pressure, lack of competitors, and high lizard densities.

Key words: burst speed, blood parasites, ectoparasites, body condition, islands, predation pressure, Lilford's Wall Lizard, *Podarcis lilfordi*.

Résumé : Les parasites peuvent avoir une incidence négative sur la performance locomotrice de leurs hôtes et, du coup, l'aptitude biologique de ces derniers. Nous examinons le lien entre le parasitisme et la vitesse de pointe dans une population insulaire de lézards de Lilford (*Podarcis lilfordi* (Günther, 1874)). *Podarcis lilfordi* est normalement infecté par des parasites sanguins hémogrégariens et des acariens dans la zone d'étude, l'île Aire (Baléares, Espagne). Contrairement aux résultats d'autres études sur des lézards, nous avons noté une corrélation négative significative entre l'intensité de l'infection aux hémogrégariens et la vitesse de pointe. L'état d'embonpoint est également significativement relié à cette vitesse. Ainsi, les lézards présentant une charge sanguine en parasites relativement faible et un meilleur état d'embonpoint ont une vitesse de pointe plus grande. L'intensité de l'infection aux hémoparasites n'est pas corrélée à l'état d'embonpoint, ni à la charge d'acariens. Nos résultats sont comparés à des résultats portant sur d'autres espèces de lézards vivant dans des habitats différents. Nous abordons l'influence des conditions ambiantes insulaires, telles que la faible pression de prédation, l'absence de concurrents et la densité élevée de lézards, sur la performance locomotrice. [Traduit par la Rédaction]

Mots-clés : vitesse de pointe, parasites sanguins, ectoparasites, état d'embonpoint, îles, pression de prédation, lézard de Lilford, *Podarcis lilfordi*.

Introduction

Locomotor capabilities, such as the maximal sprint speed or burst speed, are good indicators of performance abilities (Robson and Miles 2000). In addition, there is a clear link between locomotor performance and individuals' fitness based on the influence of locomotor capacities on foraging efficiency (Huey and Pianka 1981; Magnusson et al. 1985), escape from predators (Shine 1980; Bauwens and Thoen 1981; Webb 1986), and agonistic interactions among conspecifics (Trivers 1976; Pough and Andrews 1985; Robson and Miles 2000). There have been few studies that have looked for an association between parasitism and locomotor capabilities (e.g., mammals: Brown et al. 1994 and Hrdá et al. 2000; birds: Barbosa et al. 2002 and Møller et al. 2004; reptiles: Sorci et al. 1994 and Brown et al. 2006); not all of them have successfully found such an association. In reptiles, Oppliger et al. (1996) found that intensity of infection by haemogregarines was inversely linked to locomotor speed in the Viviparous or Common Lizard (*Zootoca vivipara* (Lichtenstein, 1823); formerly *Lacerta vivipara* Lichtenstein, 1823). Main and Bull (2000) documented this correlation in juveniles of Bobtail Lizards (*Tiliqua rugosa* (Gray, 1825)) infected with ectoparasites. In both studies, burst speed decreases as parasite

load increases. According to Schall et al. (1982), the activity in malarious lizards should be reduced because their aerobic scope is reduced. In their study, they found that although burst speed for noninfected lizards was slightly higher (1–2 s), parasitism did not have any significant effects on burst speed; however, parasitism did have obvious effects on running stamina.

The Lilford's Wall Lizard (*Podarcis lilfordi* (Günther, 1874)) is an endemic lacertid lizard of the Balearic Islands (Spain). On Aire Island, low predation pressure, high lizard density, and scarcity of food resources favour physical contact and agonistic interactions among conspecifics (Garrido and Pérez-Mellado 2013a, 2013b), all of which lead to a higher chance of parasite transfer (Garrido and Pérez-Mellado 2013a, 2013b). On Aire Island, rates of parasitism by haemogregarines and mites are among the highest found in Mediterranean lizards (Garrido and Pérez-Mellado 2013a, 2013b). Because this population is exposed to a combination of different parasites, it is critical to understand how each parasite affects the performance of those they inhabit, as well as the interaction between them (Harries et al. 2001; Graham et al. 2005; Jolles et al. 2008).

In this study, we analyze the link between both haemogregarines and mites and locomotor performance of *P. lilfordi* on

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Aire Island. If predators prey upon more parasitized individuals (Temple 1987; Navarro et al. 2004; Genovart et al. 2010), then these individuals would be eliminated from the population, thus obscuring the relationship between parasites and burst speed because the data would only reflect the relationship between parasites and burst speed of the survivors. On Aire Island, predation pressure is very low (Cooper and Pérez-Mellado 2012) and heavily infested individuals are probably not excluded from the population by predators (Temple 1987; Navarro et al. 2004; Genovart et al. 2010).

In this population, we predict that the most infested individuals would run slower than less infested individuals. We also expect to find a stronger correlation between sprint speed and haemogregarine load than between sprint speed and mite load, which agrees with other studies examining the effects of parasite infestation on other aspects of lizard physiology (Oppliger et al. 1996; Sorci et al. 1996; Oppliger and Clobert 1997).

Materials and methods

Podarcis lilfordi is a medium-sized lacertid lizard (snout-vent length (SVL) of males is up to 81 mm and SVL of females is 75 mm; Pérez-Mellado 1998). The study was conducted during June 2011 on Aire Island. Lizard density can be very high, over 4000 individuals/ha (Pérez-Mellado et al. 2008).

The term haemogregarine refers to coccidial blood parasites of the family Haemogregarinidae, containing the genera *Hepatozoon* Miller, 1908, *Haemogregarina* Danilewsky, 1885, and *Karyolysus* Labbé, 1894 (Telford 2008). Roca and Galdón (2010) suggested that blood parasites from lacertid lizards of the Iberian Peninsula and Canary Islands are from either the genus *Hepatozoon* or the genus *Hemolivia* Petit, Landau, Baccam and Lainson, 1990.

Mites of the genus *Ophionyssus* Mégnin, 1883 (Acari; Mesostigmata; Macronyssidae) are mainly parasites of Squamata. This genus includes 15 species, 13 of them confined to lizards of various genera (Fain and Bannert 2000). Lacertid lizards are parasitized by six species of *Ophionyssus*, two of them (*Ophionyssus gallotocolus* Fain and Bannert, 2000 and *Ophionyssus setosus* Fain and Bannert, 2000) are parasites of the genus *Gallotia* Boulenger, 1916 from Canary Islands (Bannert et al. 2000). In the case of the genus *Podarcis* from Spain or the rest of the Mediterranean basin, we are not aware of any taxonomic studies regarding their ectoparasites. Nevertheless, *Ophionyssus* is present in many other lizard species from the Iberian Peninsula (Bannert et al. 2000; Moraza et al. 2009; Majláthová et al. 2010) and in other *Podarcis* species from Europe (Strijbosch et al. 1980). The ectoparasites of this study were tentatively assigned to this genus.

Lizards were collected by noosing on sunny days, between 0800 and 1200 GMT, when lizards were most active. Burst speed and factors that affect it often differ depending on age or sex (e.g., Husak and Fox 2006). Therefore, to minimize this potential variation, we used only adult male lizards. Body temperatures of individuals were measured immediately after being captured and before performance trials. For each individual, we recorded SVL, body mass, and right and left hind-limb lengths (HLL). Relative sizes of hind limbs (rHLL) were calculated from the residuals of the regression of log-transformed mean value of left and right HLLs versus log-transformed SVL.

Trials were done in the field right after capture. Locomotor performance trials were carried out on a race track with a cork substrate. Two marks separated by 2 m defined the start and the end of the run (see a full description of the apparatus in Cooper et al. 2004). Two observers timed, with digital stopwatches, the time taken by the lizards to run between these two marks. Quality of each run was classified as “good” or “poor” (van Berkum and Tsuji 1987; Husak 2006). Poor runs (runs where the lizard pauses or turns back) were discarded. We included three good runs for each individual. One problem when measuring sprint speed on a

Table 1. Variance inflation factor (VIF) of variables introduced in the model to analyze their effect on burst speed of adult male Lilford’s Wall Lizards (*Podarcis lilfordi*) on Aire Island.

	Hemogregarine load	Mite load	Body condition	rHLL	SVL
VIF	1.44	1.15	1.29	1.12	1.35

Note: VIF was <3 in all cases, indicating no collinearity (Zuur et al. 2010). rHLL, relative sizes of hind limbs; SVL, snout-vent length.

race track is the difficulty in correcting for differences among individuals in their motivation to run (Sorci et al. 1995). Thus, after three poor runs, individuals were excluded from the analysis. In the analysis, we used the fastest run of each individual.

Body condition was estimated from the residuals of the regression of log-transformed body mass versus log-transformed SVL. We also counted the number of ectoparasites observed on the body surface immediately after being captured. To obtain blood samples, we made a tiny lengthwise cut on the dorsal side of the tail with a sterile scalpel. With the blood drop, we obtained a blood smear in situ. Blood smears were placed on microscopic slides and air-dried in the field. In the laboratory, slides were fixed with absolute methanol for 10 min and then stained with a modified Giemsa for 20 min. Samples were analyzed using an optical microscope at a magnification of $\times 400$. Blood parasites were haemogregarines (see above). The intensity of parasitism was estimated from a total of 2000 counted cells per sample. Lizards were always released at the locations where they were captured.

The statistical analyses were performed in the R environment (version 2.12.1; R Development Core Team 2010). We carried out a multiple linear regression analysis (Quinn and Keough 2002) to determine which variables were the most related to burst speed. Variables analyzed included haemogregarine load, mite load, and body condition. We also measured rHLL and SVL, as they could influence burst speed (Bauwens et al. 1995 and references therein). Both haemogregarine and mite load values were square-root-transformed to meet the assumptions of normality. We tested for collinearity of the explanatory variables and discarded any variable with a variance inflation factor (VIF) > 3 (Zuur et al. 2010). All variables had VIF values lower than this threshold value (Table 1), so all variables were further considered, resulting in a final set of five variables.

From a large sample of lizards studied between 2007 and 2010 in the same population, parasite load and body condition of adult males were negatively correlated (Garrido and Pérez-Mellado 2013b). In that study, we found parasite load to be higher and body condition to be lower during the summer. Moreover, these differences only appeared when body condition was categorized according to the methodology of Schall and Pearson (2000). Further analysis of data from Garrido and Pérez-Mellado (2013b) showed that during spring, when the present study was carried out, there were no differences in parasitic infection among lizards in better and worse condition. Differences appeared only during the summer. Furthermore, in another study carried out on the same population (Garrido and Pérez-Mellado 2013a), we found no relationship between parasite load and body condition. The most parasitized and larger individuals also showed better body condition. Therefore, the ecological relationship between both variables is complex on Aire Island and deserves a more detailed study; we cannot conclude that parasite load affects body condition of lizards. In the current study, no correlation was found between both variables as shown by VIF values in Table 1.

Because mites can act as vectors of haemogregarines (Telford 2008), both parasites should be positively associated. However, based on our results of the collinearity test, we discarded any relationship between both variables in our data (VIF < 3 in all cases; see Table 1). In addition, an additional study conducted on the same population (Garrido and Pérez-Mellado 2013a) showed

Table 2. Partial *F* statistic values of each predictor of burst speed in adult male Lilford's Wall Lizards (*Podarcis lilfordi*) on Aire Island at different stages of the additive model construction following a forward selection (Quinn and Keough 2002).

	Hemogregarine load	Body condition	Mite load	rHLL	SVL
Null model	4.43	1.40	0.88	0.89	1.44
Haemogregarine load		4.55	0.83	1.62	0.19
Haemogregarine load + body condition			1.45	0.85	0.01
Haemogregarine load + body condition + mite load				2.00	0
Haemogregarine load + body condition + mite load + rHLL					0.18

Note: Inclusion of predictors in the model (from left to right) at each step was done according to highest value of partial *F* statistic (Quinn and Keough 2002). Predictor included at each step are set in italic type. rHLL, relative sizes of hind limbs; SVL, snout-vent length.

Table 3. Results of the multiple regression (minimum adequate model) for burst speed in adult male Lilford's Wall Lizards (*Podarcis lilfordi*) on Aire Island.

	df	SS	MS	<i>F</i>	Pr > <i>F</i>	Slope
Haemogregarine load	1	10.59	10.59	4.71	0.036*	-0.541
Body condition	1	14.37	14.37	6.39	0.016*	0.063
Mite load	1	5.92	5.92	2.64	0.112	-0.117
rHLL	1	4.71	4.71	2.09	0.156	0.214
Body condition × rHLL	1	6.58	6.58	2.93	0.095	0.020
Residuals	39	87.67	87.67			

Note: SS, sum of squares; MS, mean square; rHLL, relative sizes of hind limbs; SVL, snout-vent length. *, *P* < 0.05.

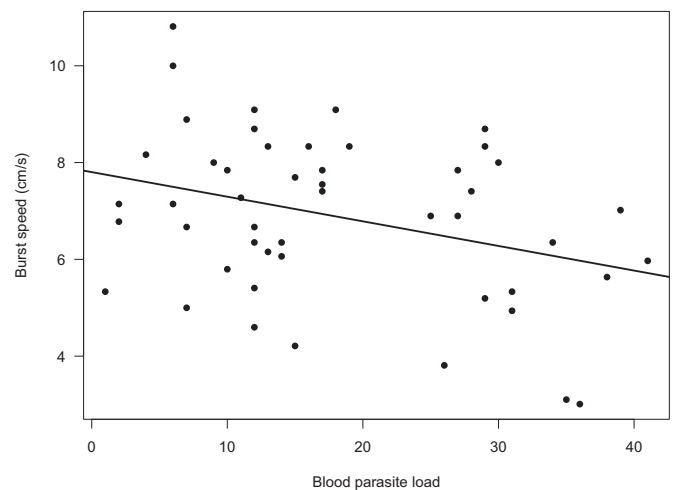
no correlation between both types of parasites. Thus, we have no evidence to support the correlation between parasites in our population of lizards.

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 and Keough 2002). In light of this, we fitted an additive model that took into account the effects of all independent variables and used forward selection to add, consecutively, the variables with the greatest *F* statistic (Quinn and Keough 2002). We then 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 Akaike's information criterion (AIC) and the Bayesian information criterion (BIC) (Quinn and Keough 2002). In all cases, effect size was reported for significant continuous predictors included in the final model as partial correlation coefficients (*r*) (Nakagawa and Cuthill 2007).

Results

Measures of burst speed taken by both observers were highly correlated, indicating high reproducibility (Spearman's rank correlation test, *R*_s = 0.64, *n* = 49, *P* = 1.55 × 10⁻⁶). Therefore, in the statistical analyses, we employed those measures taken by the observer of the fastest trials. Body temperature of lizards ranged between 31.30 and 38.30 °C (35.74 ± 0.45 °C, mean ± SE). During trials, we did not detect any significant influence of body temperature on the maximum speed of lizards (Spearman's rank correlation test, *R*_s = -0.21, *n* = 30, *P* = 0.15). HLL values ranged between 32.36 and 40.36 mm (36.52 ± 0.27 mm, mean ± SE) and body size ranged between 59.00 and 76.00 mm (69.99 ± 0.55 mm, mean ± SE).

Following the forward selection procedure, we started with a null model and introduced, at each step, the predictor with the highest partial *F* statistic value (Quinn and Keough 2002). Therefore, we first added haemogregarine load, followed by body condition, mite load, and rHLL, respectively (Table 2). Up to this point, having included each predictor, AIC and BIC values were reduced and the value of the adjusted *r*² was increased. With the inclusion of body size, AIC and BIC values increased and the value of adjusted *r*² decreased (before SVL inclusion, adjusted *r*² = 0.20, AIC = 172.97, BIC = 183.81; after SVL inclusion, adjusted *r*² = 0.18, AIC =

Fig. 1. Relationship between burst speed and blood parasite load in Lilford's Wall Lizard (*Podarcis lilfordi*). Partial correlation coefficient showed a medium-sized effect of blood parasite load, which was nearly large in effect (*r* = 0.45).

174.77, BIC = 187.42), so we decided to exclude SVL from the additive model.

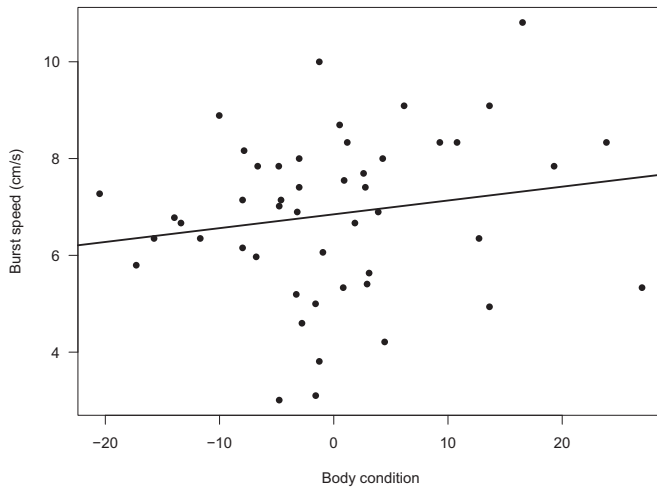
The saturated model, including interactions between previously introduced variables (mite and haemogregarine load, body condition, and rHLL), showed worse values for the three estimators (adjusted *r*² = 0.08, AIC = 186.85, BIC = 217.56), consequently this model was discarded (Quinn and Keough 2002). Only the inclusion of the interaction between body condition and rHLL improved the additive model. The remaining interactions showed a *P* value above 0.05 (all *F* < 0.60). With the inclusion of this interaction term, BIC was slightly higher (184.36), but AIC (171.72) and adjusted *r*² (0.24) showed better values.

The final model (Table 3) revealed that neither ectoparasite load nor rHLL and its interaction with body condition were related to burst speed of lizards, although they were retained in the model (Table 3). Only the intensity of infection by haemogregarines and body condition were significantly linked to burst speed (Table 3). Both predictors showed a medium-sized effect, being larger for haemogregarine load (*r* = 0.45 compared with *r* = 0.36 for body condition). Therefore, burst speed was higher for lizards with a lower blood parasite load and a better body condition (Figs. 1, 2).

Discussion

According to our predictions, we found an important negative relationship between blood parasite load and running speed. Haemogregarines may reduce hosts' haemoglobin concentrations, lowering their capacity for oxygen transportation to muscle tissue (Oppliger et al. 1996). Therefore, several physiological and behavioural traits of hosts, such as foraging efficiency, could be affected (Caudell et al. 2002). In the present study, less parasitized

Fig. 2. Relationship between burst speed and body condition in Lilford's Wall Lizard (*Podarcis lilfordi*). Partial correlation coefficient showed a medium-sized effect of body condition ($r = 0.36$).



individuals by haemogregarines and those individuals with a better body condition ran faster. For both predictors, we documented a medium-sized effect, the larger effect being for parasite load.

Oppliger et al. (1996) also found a detrimental effect of blood parasites on burst speed of *Z. vivipara*. However, we did not find any other study that successfully related haemoparasite load with burst speed in reptiles (e.g., Schall 1982, Salkeld 2004, Brown et al. 2006, or Ekner-Grzyb et al. 2013). Predators usually capture the most parasitized individuals (Temple 1987), which suggests that most parasitized lizards may be more vulnerable to predation because their mobility is reduced (Oppliger et al. 1996). In general, it is thought that high speed and endurance have positive effects on one's ability to escape from predators (Clobert et al. 2000 and references therein). Therefore, the most parasitized lizards are eliminated from the population by predators, turning the relationship between parasites and burst speed into an obscure one. On Aire Island, predation risk on *P. lilfordi* is very low and this problem can be avoided.

In continental populations, the detrimental effects of parasitism are more evident because of the presence of predators or competitor species: either by direct predation on the most parasitized (Temple 1987; Navarro et al. 2004; Genovart et al. 2010) or indirectly through the costs of performing escape responses (Amo et al. 2007) or the redistribution of resources in the presence of predators (Navarro et al. 2004). On Aire Island, predation pressure is low and there is a lack of terrestrial competitors. In such ecological context, although parasites affect running speed or escape behaviour (M. Garrido and V. Pérez-Mellado, unpublished data), the effects are not as critical as they might be on a continental population. Furthermore, in our study population, parasitism per se does not require significant energy costs from the hosts, as reflected by the lack of correlation with body condition (Garrido and Pérez-Mellado 2013a).

Our results showed no influence of ectoparasite load on running speed. In laboratory trials, *T. rugosa* infested by mites ran slower and had a lower endurance (Main and Bull 2000). With the exception of Main and Bull's (2000) study, no correlation of locomotor performance and ectoparasites was documented for reptiles in natural populations. Dunlap and Mathies (1993) found harmful effects of mites only when lizards were co-infected with other parasites such as those that cause malaria. In the present study, the interaction of parasites did not influence maximal running speed of lizards on Aire Island. Additionally, as haemogregarines are vector-borne parasites (Telford 2008), haemogregarines and mites should be positively associated. However, we

did not find such a correlation (see Materials and methods), even in an earlier study conducted on the same population (Garrido and Pérez-Mellado 2013a). These results are in accordance with other studies conducted on lacertid lizards (e.g., Amo et al. 2005; García-Ramírez et al. 2005). The lack of a relationship does not necessarily imply that mites are not haemogregarine vectors. It could arise from differences in the etiology, dynamics, and other factors affecting each infection.

Several studies concluded that parasitism was the major cause for the loss of fitness capabilities (Temple 1987; Navarro et al. 2004; Genovart et al. 2010 and references therein). In reptiles, blood parasites seem to have several consequences: decreasing the maximal sprint speed of their host (Oppliger et al. 1996), decreasing the resting metabolic rate (Oppliger et al. 1996), and increasing their reproductive effort (Sorci et al. 1996), as well as perturbing the ability to regenerate the tail after autotomy (Oppliger and Clobert 1997). Schall et al. (1982) observed blood parasites of the genus *Plasmodium* Marchiafava and Celli, 1885 affecting the physiology, behaviour, and reproductive success of several lizard species such as the Western Fence Lizard (*Sceloporus occidentalis* Baird and Girard, 1852), Common Agama (*Agama agama* (L., 1758)), Anguilla Bank Anole (*Anolis gingivinus* Cope, 1865), and Watts' Anole (*Anolis watti* Boulenger, 1894). However, there are significantly fewer examples regarding consequences of ectoparasites (Main and Bull, 2000). Effects of mites seem to be more evident in the offsprings of parasitized hosts (Sorci et al. 1994; Sorci and Clobert 1995).

Finally, in the present study, we were unable to find a direct relationship between burst speed and rHLL. The predictions of biomechanical models and other studies on lacertid lizards showed a positive relationship between rHLL and burst speed (Bauwens et al. 1995). Accordingly, morphology had a high explanatory power in multispecies comparisons (Pounds 1988; Bauwens et al. 1995; Bonine and Garland 1999; Van Damme and Vanhooydonck 2001). However, at an intraspecific level, several studies showed the weakness of this relationship (Garland 1985; Van Damme et al. 1997; Macrini and Irschick 1998).

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References

- Amo, L., López, P., and Martín, J. 2005. Prevalence and intensity of haemogregarine blood parasites and their mite vectors in the common wall lizard, *Podarcis muralis*. *Parasitol. Res.* **96**: 378–381. doi:10.1007/s00436-005-1354-2. PMID: 15940525.
- Amo, L., Lopez, P., and Martin, J. 2007. Habitat deterioration affects body condition of lizards: a behavioral approach with *Iberolacerta cyreni* lizards inhabiting ski resorts. *Biol. Conserv.* **135**(1): 77–85. doi:10.1016/j.biocon.2006.09.020.
- Bannert, B., Karaca, H.Y., and Wohltmann, A. 2000. Life cycle and parasitic interaction of the lizard-parasitizing mite *Ophionyssus gallotocolus* (Acari: Gamasida: Macronyssidae), with remarks about the evolutionary consequences of parasitism in mites. *Exp. Appl. Acarol.* **24**: 597–613. doi:10.1023/A:1026504627926. PMID:11201353.
- Barbosa, A., Merino, S., Lope, F., and Møller, A.P. 2002. Effects of feather lice on flight behavior of male Barn Swallows (*Hirundo rustica*). *Auk*, **119**(1): 213–216. doi:10.1642/0004-8038(2002)119[0213:EOFLOF]2.0.CO;2.

- Bauwens, D., and Thoen, C. 1981. Escape tactics and vulnerability to predation associated with reproduction in the lizard *Lacerta vivipara*. *J. Anim. Ecol.* **50**: 733–743. doi:10.2307/4133.
- Bauwens, D., Garland, T., Jr., Castilla, A.M., and Van Damme, R. 1995. Evolution of sprint speed in lacertid lizards: morphological, physiological, and behavioral covariation. *Evolution*, **49**: 848–863. doi:10.2307/2410408.
- Bonine, K.E., and Garland, T., Jr. 1999. Sprint performance of phrynosomatid lizards, measured on a high-speed treadmill, correlates with hindlimb length. *J. Zool. (Lond.)*, **248**: 255–265. doi:10.1111/j.1469-7998.1999.tb011201.x.
- Brown, G.P., Shilton, C.M., and Shine, R. 2006. Do parasites matter? Assessing the fitness consequences of haemogregarine infection in snakes. *Can. J. Zool.* **84**(5): 668–676. doi:10.1139/z06-044.
- Brown, E.D., Macdonald, D.W., Tew, T.E., and Todd, I.A. 1994. *Apodemus sylvaticus* infected with *Heligmosomoides polygyrus* (Nematoda) in an arable ecosystem: epidemiology and effects of infection on the movements of male mice. *J. Zool. (Lond.)*, **234**: 623–640. doi:10.1111/j.1469-7998.1994.tb04869.x.
- Caudell, J.N., Whittier, J., and Conover, M.R. 2002. The effects of haemogregarine-like parasites on brown tree snakes (*Boiga irregularis*) and slatey-grey snakes (*Stegonotus cucullatus*) in Queensland, Australia. *Int. Biodet. Biodegrad.* **49**: 113–119. doi:10.1016/S0964-8305(01)00111-1.
- Clobert, J., Oppliger, A., Sorci, G., Ernande, B., Swallow, J.G., and Garland, T. 2000. Trade-offs in phenotypic traits: endurance at birth, growth, survival, predation and susceptibility to parasitism in a lizard, *Lacerta vivipara*. *Funct. Ecol.* **14**(6): 675–684. doi:10.1046/j.1365-2435.2000.00477.x.
- Cooper, W.E., Jr., and Pérez-Mellado, V. 2012. Historical influence of predation pressure on escape by *Podarcis* lizards in the Balearic Islands. *Biol. J. Linn. Soc.* **107**: 254–268. doi:10.1111/j.1095-8312.2012.01933.x.
- Cooper, W.E., Jr., Pérez-Mellado, V., and Vitt, L.J. 2004. Ease and effectiveness of costly autotomy vary with predation intensity among lizard populations. *J. Zool. (Lond.)*, **262**: 243–255. doi:10.1017/S095283690300462X.
- Dunlap, K.D., and Mathies, T. 1993. Effects of nymphal ticks and their interaction with malaria on the physiology of male fence lizards. *Copeia*, **1993**: 1045–1048. doi:10.2307/1447082.
- Ekner-Grzyb, A., Sajkowska, Z., Dudek, K., Gawalek, M., Skórka, P., and Tryjanowski, P. 2013. Locomotor performance of sand lizards (*Lacerta agilis*): effects of predatory pressure and parasite load. *Acta Ethol.* **16**: 173–179. doi:10.1007/s10211-012-0131-3.
- Fain, A., and Bannert, B. 2000. Two new species of *Ophionyssus* Mégnin (Acari: Macronyssidae) parasitic on lizards of the genus *Gallotia* Boulenger (Reptilia: Lacertidae) from the Canary Islands. *Int. J. Acarol.* **26**(1): 41–51. doi:10.1080/01647950008683634.
- García-Ramírez, A., Delgado-García, J.D., Foronda-Rodríguez, P., and Abreu-Acosta, N. 2005. Haematozoans, mites and body condition in the oceanic island lizard *Gallotia atlantica* (Peters and Doria, 1882) (Reptilia: Lacertidae). *J. Nat. Hist.* **39**: 1299–1305. doi:10.1080/00222930400015590.
- Garland, T., Jr. 1985. Ontogenetic and individual variation in size, shape and speed in the Australian agamid lizard *Amphibolurus nuchalis*. *J. Zool. (Lond.)*, **207**: 425–439. doi:10.1111/j.1469-7998.1985.tb04941.x.
- Garrido, M., and Pérez-Mellado, V. 2013a. Patterns of parasitism in insular lizards: effects of body size, condition and resource availability. *Zoology*, **116**(2): 106–112. doi:10.1016/j.zool.2012.09.003.
- Garrido, M., and Pérez-Mellado, V. 2013b. Prevalence and intensity of blood parasites in insular lizards. *Zool. Anz.* **252**(4): 588–592. doi:10.1016/j.jcz.2012.11.003.
- Genovart, M., Negre, N., Tavecchia, G., Bistuer, A., Parpal, L., and Oro, D. 2010. The young, the weak and the sick: evidence of natural selection by predation. *PLoS ONE*, **5**: e9774. doi:10.1371/journal.pone.0009774. PMID:20333305.
- Graham, A.L., Lamb, T.J., Read, A.F., and Allen, J.E. 2005. Malaria-filariasis co-infection in mice makes malarial disease more severe unless filarial infection achieves patency. *J. Infect. Dis.* **191**: 410–421. doi:10.1086/426871. PMID:15633101.
- Harries, A.D., Hargreaves, N.J., Kemp, J., Jindani, A., Enarson, D.A., Maher, D., and Salaniponi, F.M. 2001. Deaths from tuberculosis in sub-Saharan African countries with a high prevalence of HIV-1. *Lancet*, **357**: 1519–1523. doi:10.1016/S0140-6736(00)04639-0. PMID:11377627.
- Hrdá, Š., Votýpka, J., Kodym, P., and Flegl, J. 2000. Transient nature of *Toxoplasma gondii*-induced behavioral changes in mice. *J. Parasitol.* **86**(4): 657–663. doi:10.1645/0022-3395(2000)086[0657:TNOTG]2.0.CO;2. PMID:10958436.
- Huey, R.B., and Pianka, E.R. 1981. Ecological consequences of foraging mode. *Ecology*, **62**: 991–999. doi:10.2307/1936998.
- Husak, J.F. 2006. Does survival depend on how fast you can run or how fast you do run? *Funct. Ecol.* **20**: 1080–1086. doi:10.1111/j.1365-2435.2006.01195.x.
- Husak, J.F., and Fox, S.F. 2006. Field use of maximal sprint speed by collared lizards (*Crotaphytus collaris*): compensation and sexual selection. *Evolution*, **60**(9): 1888–1895. doi:10.1111/j.0014-3820.2006.tb00532.x. PMID:17089973.
- Jolles, A.E., Ezenwa, V.O., Etienne, R.S., Turner, W.C., and Oliff, H. 2008. Interactions between macroparasites and microparasites drive infection patterns in free-ranging African buffalo. *Ecology*, **89**: 2239–2250. doi:10.1890/07-0995.1. PMID:18724734.
- Macrini, T.E., and Irschick, D.J. 1998. An intraspecific analysis of trade-offs in sprinting performance in a West Indian lizard species (*Anolis lineatopus*). *Biol. J. Linn. Soc.* **63**: 579–591. doi:10.1111/j.1095-8312.1998.tb00330.x.
- Magnusson, W.E., Junqueira de Paiva, L., Moreira da Rocha, R., Franke, C.R., Kasper, L.A., and Lima, A.P. 1985. The correlates of foraging mode in a community of Brazilian lizards. *Herpetologica*, **41**: 324–332.
- Main, A.R., and Bull, C.M. 2000. The impact of tick parasites on the behaviour of the lizard *Tiliqua rugosa*. *Oecologia*, **122**: 574–581. doi:10.1007/s004420050981.
- Majláthová, V., Majláth, I., Haklová, B., Hromada, M., Ekner, A., Antczak, M., and Tryjanowski, P. 2010. Blood parasites in two co-existing species of lizards (*Zootoca vivipara* and *Lacerta agilis*). *Parasitol. Res.* **107**: 1121–1127. doi:10.1007/s00436-010-1981-0. PMID:20661747.
- Møller, A.P., de Lope, F., and Saino, N. 2004. Parasitism, immunity, and arrival date in a migratory bird, the barn swallow. *Ecology*, **85**(1): 206–219. doi:10.1890/02-0451.
- Moraza, M.L., Irwin, N.R., Godinho, R., Baird, S.J.E., and De Belloq, J.G. 2009. A new species of *Ophionyssus* Mégnin (Acari: Mesostigmata: Macronyssidae) parasitic on *Lacerta schreiberi* Bedriaga (Reptilia: Lacertidae) from the Iberian Peninsula, and a world key to species. *Zootaxa*, **2007**: 58–68.
- Nakagawa, S., and Cuthill, I.C. 2007. Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biol. Rev.* **82**(4): 591–605. doi:10.1111/j.1469-185X.2007.00027.x. PMID:17944619.
- Navarro, C., de Lope, F., Marzal, A., and Møller, A.P. 2004. Predation risk, host immune response, and parasitism. *Behav. Ecol.* **15**: 629–635. doi:10.1093/beheco/ahr054.
- Oppliger, A., and Clobert, J. 1997. Reduced tail regeneration in the common lizard, *Lacerta vivipara*, parasitized by blood parasites. *Funct. Ecol.* **11**: 652–655. doi:10.1046/j.1365-2435.1997.00134.x.
- Oppliger, A., Célérier, M.L., and Clobert, J. 1996. Physiological and behaviour changes in common lizards parasitized by haemogregarines. *Parasitology*, **113**: 433–438. doi:10.1017/S003118200008149X.
- Pérez-Mellado, V. 1998. *Podarcis lilfordi* (Günther, 1874). In *Fauna Ibérica*. Vol. 10. Edited by A. Salvador. Museo Nacional de Ciencias Naturales, Madrid. pp. 272–282.
- Pérez-Mellado, V., Hernández-Estévez, J.A., García-Díez, T., Terrasa, B., Ramón, M.M., Castro, J., Picornell, A., Martín-Vallejo, J., and Brown, R. 2008. Population density in *Podarcis lilfordi* (Squamata, Lacertidae), a lizard species endemic to small islets in the Balearic Islands (Spain). *Amphib.-Reptilia*, **29**: 49–60. doi:10.1163/156853808783431587.
- Pough, F.H., and Andrews, R.M. 1985. Use of anaerobic metabolism by free-ranging lizards. *Physiol. Zool.* **58**: 205–213.
- Pounds, J.A. 1988. Ecomorphology, locomotion, and microhabitat structure: patterns in a tropical mainland *Anolis* community. *Ecol. Monogr.* **58**: 299–320. doi:10.2307/1942542.
- Quinn, G.P., and Keough, M.J. 2002. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge, UK.
- R Development Core Team. 2010. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from <http://www.r-project.org/>.
- Robson, M.A., and Miles, D.B. 2000. Locomotor performance and dominance in male Tree Lizards, *Urosaurus ornatus*. *Funct. Ecol.* **14**: 338–344. doi:10.1046/j.1365-2435.2000.00427.x.
- Roca, V., and Galdón, M.A. 2010. Haemogregarine blood parasites in the lizards *Podarcis bocagei* (Seoane) and *P. carbonelli* (Pérez-Mellado) (Sauria: Lacertidae) from NW Portugal. *Syst. Parasitol.* **75**: 75–79. doi:10.1007/s11230-009-9206-6. PMID:20012520.
- Salkeld, D.J. 2004. The ecology of a host–parasite relationship: haemogregarines and the eastern water skink, *Eulamprus quoyii*. Ph.D. thesis, James Cook University, Townsville, Australia.
- Schall, J.J., and Pearson, A.R. 2000. Body condition of a Puerto Rican anole, *Anolis gundlachi*: effect of a malaria parasite and weather variation. *J. Herpetol.* **34**: 489–491. doi:10.2307/1565380.
- Schall, J.J., Bennett, A.F., and Putnam, R.W. 1982. Lizards infected with malaria: physiological and behavioral consequences. *Science*, **217**: 1057–1059. doi:10.1126/science.7112113. PMID:7112113.
- Shine, R. 1980. “Costs” of reproduction in reptiles. *Oecologia*, **46**: 92–100. doi:10.1007/BF00346972.
- Sorci, G., and Clobert, J. 1995. Effects of maternal parasite load on offspring life-history traits in the common lizard (*Lacerta vivipara*). *J. Evol. Biol.* **8**: 711–723. doi:10.1046/j.1420-9101.1995.8060711.x.
- Sorci, G., Massot, M., and Clobert, J. 1994. Maternal parasite load increases sprint speed and philopatry in female offspring of the common lizard. *Am. Nat.* **144**(1): 153–164. doi:10.1086/285666.
- Sorci, G., Swallow, J.G., Garland, T., Jr., and Clobert, J. 1995. Quantitative genetics of locomotor speed and endurance in the lizard *Lacerta vivipara*. *Physiol. Zool.* **68**: 698–720.
- Sorci, G., Clobert, J., and Michalakis, Y. 1996. Cost of reproduction and cost of parasitism in the common lizard, *Lacerta vivipara*. *Oikos*, **76**: 121–130. doi:10.2307/3545754.
- Strijbosch, H., Bonnemayer, J.J.A.M., and Dietvorst, P.J.M. 1980. The northernmost population of *Podarcis muralis* (Lacertilia, Lacertidae). *Amphib.-Reptilia*, **1**: 161–172. doi:10.1163/156853880X001050.
- Telford, S.R. 2008. Hemoparasites of the Reptilia: color atlas and text. CRC Press, Boca Raton, Fla.
- Temple, S.A. 1987. Do predators always capture substandard individuals disproportionately from prey populations? *Ecology*, **68**: 669–674. doi:10.2307/1938472.

- Trivers, R.L. 1976. Sexual selection and resource-accruing abilities in *Anolis garmani*. *Evolution*, **30**: 253–267. doi:[10.2307/2407700](https://doi.org/10.2307/2407700).
- Van Damme, R., and Vanhooydonck, B. 2001. Origins of interspecific variation in lizard sprint capacity. *Funct. Ecol.* **15**: 186–202. doi:[10.1046/j.1365-2435.2001.00513.x](https://doi.org/10.1046/j.1365-2435.2001.00513.x).
- Van Damme, R., Aerts, P., and Vanhooydonck, B. 1997. No tradeoff between sprinting and climbing in two populations of the lizard *Podarcis hispanica* (Reptilia: Lacertidae). *Biol. J. Linn. Soc.* **60**: 493–503. doi:[10.1006/bijl.1996.0115](https://doi.org/10.1006/bijl.1996.0115).
- van Berkum, F.H., and Tsuji, J.S. 1987. Inter-familial differences in sprint speed of hatchling *Sceloporus occidentalis* (Reptilia: Iguanidae). *J. Zool. (Lond.)*, **212**: 511–519. doi:[10.1111/j.1469-7998.1987.tb02921.x](https://doi.org/10.1111/j.1469-7998.1987.tb02921.x).
- Webb, P.W. 1986. Locomotion and predator–prey relationships. In *Predator–prey relationships: perspectives and approaches from the study of lower vertebrates*. Edited by M.E. Feder and G.V. Lauder. University of Chicago Press, Chicago. pp. 24–41.
- Zuur, A.F., Ieno, E.N., and Elphick, C.S. 2010. A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* **1**(1): 3–14. doi:[10.1111/j.2041-210X.2009.00001.x](https://doi.org/10.1111/j.2041-210X.2009.00001.x).