

RESEARCH ARTICLE

Are whole-organism performance and thermal preference linked to endo- and ectoparasites in a short-lived lizard?

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Funding information

Macquarie University

Editor: Wolfgang Goymann

Abstract

Wild animals are often concurrently infected by multiple parasites, which are assumed to negatively affect their host by exploiting the host's resources. The cumulative effect of parasite infections is often not studied. Despite this assumption, many hosts do not suffer significant costs from parasitism in the wild. Hosts can adapt to parasitic infections by mounting physiological and behavioural defences. A commonly used behavioural defence by ectotherms is to frequently visit warm environments to increase body temperature (i.e., behavioural fever) and thereby mount an immune response to parasites. Using the Australian common garden skink (*Lampropholis guichenoti*), we investigated the cumulative effect of endo- and ectoparasites on host performance. First, we investigated whether endo- and ectoparasites were associated with whole-organism performance in the lizards. Second, we explored whether host individuals responded to their parasite infection through thermoregulatory behaviour. We found no significant relationship between parasitism and body condition. However, the infection with ectoparasitic mites was significantly related to reduced sprint speed, while the nematode infection had no significant relationship with any of our three performance measures (sprint speed, endurance and foraging efficiency). We showed no evidence of behavioural fever and infected lizards did not differ in their body temperature from uninfected lizards. Our findings suggest that short-lived lizards may simply endure parasitic infections. The study provides an important example of how multiple infections with endo- and ectoparasites affect their host. It adds to the growing evidence for a negligible effect of parasites on host whole-organism performance.

KEYWORDS

Acari, ascarid, locomotion, parasitism, thermoregulation

1 | INTRODUCTION

The nature of parasites is to exploit the energy of their hosts for development and replication (Mehlhorn, 2016). Parasitism is assumed to have a negative effect on host performance because it

leads to an immune or stress response, and corresponding loss of body condition in the host (Johnson et al., 1999). For instance, trematode cyst infestation impairs limb development in frogs and also causes deformities, which is disadvantageous for locomotion and survival (Cunningham et al., 2005; Goodman & Johnson, 2011;

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Stopper et al., 2002). Furthermore, parasites can affect their host's behaviour (e.g. social interaction) and performance capacity, which is the ability of an animal to execute a behaviour (Binning et al., 2017; Ezenwa & Snider, 2016). For example, captured southern flounder (*Paralichthys lethostigma*) infected by muscle nematodes had a significantly lower swimming speed than uninfected ones, and this effect was greater in smaller fish in the group (Umberger et al., 2013). In the wild, high parasite loads in cane toads (*Rhinella marina*) reduced the distance they moved and their growth rate (Finnerty et al., 2017). The majority of studies have found a negative effect of parasitism while others did not find any negative effect or even found a positive effect on the host (Sánchez et al., 2018).

A growing body of literature suggests that parasitism may often have no discernible negative effects (Bonneaud et al., 2017; Leathwick et al., 2020; Mayer et al., 2015; Paterson & Blouin-Demers, 2020). This finding may be the outcome of an evolutionary arms race that has selected hosts to cope with parasites. Body condition and whole-organism performance (e.g., movement speed and endurance) are commonly used to examine the effects of parasitism on the host (McElroy & de Buron, 2014; Sánchez et al., 2018). Body condition is a proxy for host health while whole-organism performance represents the ability to accomplish ecological tasks relevant to fitness (Irschick et al., 2008; Lailvaux & Husak, 2014). However, many parasites may not have an obvious effect on the host, which leads to a null relationship between parasite load and body condition. Parasitism generally reduces the host's whole-organism performance but non-significant results are also regularly reported (Mayer et al., 2015; McElroy & de Buron, 2014; Taggart et al., 2018). For instance, many feather mites do not have adverse effects on their host but are commensals in birds (Galván et al., 2012). Alternatively, an adverse effect of parasites may be masked whether the host behaviourally compensates for the physiological cost of parasites.

In contrast to endotherms that can activate internal fever against the infection, infected ectotherms often modify their preferred body temperature through altered basking behaviours (Rakus et al., 2017). For example, ectotherms can seek a warmer environment to up-regulate their body temperature (fever), which is referred to as "behavioural fever" (Mohammed et al., 2016; Moretti et al., 2018). The first evidence of behavioural fever in reptiles dates back nearly 50 years in desert iguanas (*Dipsosaurus dorsalis*). Lizards, after being injected with pathogenic bacteria (*Aeromonas hydrophila*), selected a warmer environment and increased their body temperature by approximately 2°C (Vaughn et al., 1974). This phenomenon has been reported in all ectothermic vertebrate taxa (Rakus et al., 2017), including reptiles (Ryan et al., 2018), amphibians (Sauer et al., 2019) and fishes (Boltaña et al., 2013). A higher preferred body temperature can enhance the innate immune response (Lin et al., 2019; Roth & Blatteis, 2011). Moreover, body temperature is positively correlated with whole-organism performance in many ectothermic animals (Goulet et al., 2017; Huey & Kingsolver, 1989; Marsh & Bennett, 1986). As a result, behavioural fever can reduce the effects of parasitism (Elliot et al., 2002).

Lizards are good model systems to study the host-parasite relationship because methods of measuring their performances have been well developed (Baxter-Gilbert et al., 2017; Gomes et al., 2017; Husak & Lailvaux, 2017; Losos et al., 2002), and their whole-organism performance capacity may relate to their fitness (Irschick et al., 2008; Lailvaux et al., 2012, 2018; Noble, McFarlane, et al., 2014). Many species also rely heavily on their performance capacity to forage, irrespective of whether they are ambush predators or active foragers (Kuo et al., 2019). Consequently, any impact on performance capacity (specifically locomotion) may also have downstream effects on foraging efficiency. Here, we examined the effects of parasitism on whole-organism performance (in particular locomotor performance and foraging efficiency) and thermal preference in common garden skinks (*Lampropholis guichenoti*). Garden skinks are host to several gastrointestinal parasites, *Eimeria lampropholidus* (Cannon, 1967), *Cylindrotaenia hickmani* (Goldberg & Bursey, 2012; Jones, 1985), *Skrjabinodon* sp., *Maxvachonia chabaudi*, *Hedroris wogwogensis* (Jones & Resasco, 2016), *Sphaerechinorhynchus rotundocapitatus* (Daniels & Simbotwe, 1984), as well as ectoparasites including mites (Trombiculidae) and hard ticks (Acari: Ixodida; Hamilton et al., 2021). However, the effects of these parasites on their host are poorly understood (Resasco et al., 2019). We asked two questions: (1) is parasitism related to whole-organism performance capacity (sprint speed, endurance and foraging efficiency)? (2) Do parasitised individuals select warmer temperatures to induce behavioural fever?

2 | MATERIALS AND METHODS

2.1 | Animal collection and husbandry

We collected 40 (20 males and 20 females) common garden skinks (*L. guichenoti*) from suburban areas near Macquarie University campus (Sydney) during March to April 2020 by hand or mealworm fishing. We applied the STRANGE framework (Webster & Rutz, 2020) to ensure that trapping method did not unduly influence our study sample (e.g., bias towards explorative individuals). Lizards were captured by hand or mealworm fishing, which limits capture bias (Michelangeli, Wong, & Chapple, 2016).

We only retained individuals with a relatively complete tail (tail length > SVL) because tail loss can affect whole-organism performance in *Lampropholis* skinks (Cromie & Chapple, 2012). We determined the sex of each lizard on the day of capture; males were identified by the presence of hemipenes. We released gravid females because pregnancy can reduce locomotor performance in lizards (Shine, 2003). We measured snout-vent length (SVL) to the nearest .01 mm with digital callipers and body weight with a digital balance (nearest .001 g). We then counted the ectoparasites on the lizards using a magnifying glass. The ectoparasites mostly gathered around the armpits of the lizard. All measurements mentioned above were done on the day of capture.

We transported them to our indoor animal facility and kept the lizards individually before the measurement of whole-organism performance capacity. We housed lizards individually in plastic containers (200 × 135 × 70 mm) to prevent cross-infection with parasites and to reduce any stress associated with sharing space with other lizards. Each lizard was provided with UV lighting above, and a heating cable (30°C) beneath a plastic shelter, thereby creating a thermal gradient (22–30°C). Lizards were able to regulate their body temperature within the thermal gradient provided by the heating cable. The room temperature was controlled at approximately 22°C and daily photoperiod was 12 hours (08:00–20:00h). We fed the lizards with captive-bred crickets three times a week and provided filtered water *ad libitum*. Crickets were dusted with vitamin supplement/calcium once per week. During the measurement of whole-organism performance capacity, the lizards were assigned to four batches of 10 lizards because our thermal gradient could only accommodate 10 lizards at a time. Lizards from different batches all went through the same sequence of experimental trials (Figure 1).

2.2 | Faecal sample examination

We collected each lizard's scat every other day to examine the infection load after they arrived at our animal facility. Fresh scats were collected by gently pressing the abdomen the morning after feeding. We only picked up moist scats because dry scats may affect egg counts in the faecal sample. We put each scat in an Eppendorf tube and stored them at 4°C before counting parasite eggs. Multiple scats from the same individual were mixed into a faecal sample to represent the infection load for a certain week. We isolated parasite eggs from the scat using saline floatation with Epsom salt solution (Garcia, 2001). We made up the Epsom salt solution by dissolving 400g of Epsom salt in 1L of distilled water. We weighed the scats using a digital balance (nearest .001g) before the saline floatation process. We floated the faecal sample in 1 mL of Epsom salt solution and gently shook the Eppendorf tube to break the big fragments in

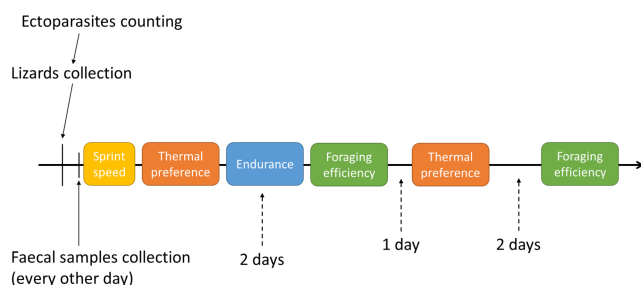


FIGURE 1 Sequence of experimental trials. On the day of capture, body size (snout-vent length) and body mass (g) were measured and ectoparasite load was recorded. Faecal samples were collected every other day starting with the second day of the experimental scheme. Sprint speed was measured first, and subsequently, thermal preference (trial 1), endurance (measured in two consecutive days), foraging efficiency (trial 1), thermal preference (trial 2) and foraging efficiency (trial 2).

the faecal sample. We took 650 ul of the supernatant and added it into a McMaster chamber. We counted parasite eggs under a binocular microscope with the McMaster chamber as the measure of infection load (eggs per gram of fresh scat; Fenner & Bull, 2008). The parasites were identified to the lowest taxonomic resolution possible (generally family level).

2.3 | Sprint speed and endurance

Lizards were fasted for 1 day prior to sprint speed and endurance trials. Before conducting trials, all lizards were warmed to their preferred temperature 30°C (Cromie & Chapple, 2012) in an incubator for 90 min. We also set the room temperature at 30°C. We weighed every lizard and measured the body temperature after the trial using a handheld infrared thermometer (Ryobi RIT310, Victoria, AU).

The racetrack was 100 × 10 cm, with 10 cm high walls, and with lines marked every 25 cm (Cromie & Chapple, 2012; Goulet et al., 2017; Lowie et al., 2019). Each lizard was measured three times per day with a 90 min interval between trials (Losos et al., 2002). Lizards were moved back to their own tub during this 90 min interval. We used a paintbrush to stimulate lizards to run by tapping on their tail. Trials were filmed using a high-speed camera (100 frames per second; Sony CMOS HDR-SR7). We calculated sprint speed using the software Tracker v5.1.5 (Open Source Physics, USA; <https://physlets.org/tracker/>). Sprint speed was assessed from when the focal lizard's snout entered and then broke the lines demarcating the 25 cm interval. We used the maximum velocity measured in the four sections as the sprint speed (cm s^{-1}) for each trial. It is worth noting that although we refer to this as 'maximum' sprint speed, we acknowledge that it is the fastest of the observed speeds but not necessarily the individual's true maximum speed. We use the term 'maximum' to be consistent with the literature on lizard performance capacity (Cromie & Chapple, 2012; Goulet et al., 2017; Losos et al., 2002; Lowie et al., 2019). The sample size of this experiment was a total of 40 lizards (20 males and 20 females).

We measured maximal endurance using a treadmill and chased the lizard until exhaustion by gently tapping on its tail with a paintbrush. Each lizard was run three times over two consecutive days (Day 1: 15:00h, Day 2: 10:30h, 15:00h). We placed a transparent plexiglass box with adjustable compartments on a treadmill (Avanti AT380). The treadmill was set to a fixed running speed of 1.0 (km/h; Baxter-Gilbert et al., 2017; Noble, Fanson, & Whiting, 2014). For the treadmill speed, we used an absolute speed instead of a relative speed (scaled to individual body length) because lizard snout-vent length showed low variation (mean SVL 40.8 mm, SD 2.5). Furthermore, this particular treadmill speed was chosen because it has been applied to other studies of scincid lizards and other lizards with similar body size (Garland Jr., 1984, 1994). This absolute speed was considered to represent the contribution of aerobic energy metabolism indicated by maximal rates of oxygen consumption (Garland Jr., 1984). The adjustable compartment meant they could run straight but could not easily turn around. We considered a lizard exhausted when it no

longer reacted to stimulation after five light taps on the base of tail. Then, it could safely fall into a container at the base of the treadmill. The time to exhaustion was recorded as the measure of endurance for each lizard (Noble, McFarlane, et al., 2014). One individual was not able to complete its third measurement, and hence, we excluded this data point from the endurance analysis. We kept data points collected from this individual in the first and the second measurement. The sample size of this experiment was a total of 40 lizards (20 males and 20 females).

2.4 | Foraging efficiency assay

Lizards were fasted for 2 days prior to measuring foraging efficiency. Each lizard was tested twice, with a 4-day interval between measurements. On the day of the trial, we weighed and warmed up lizards to their preferred body temperature of 30°C (Cromie & Chapple, 2012) in an incubator for 90 min and set the room temperature at 30°C. We introduced focal lizards into an arena with a refuge at one end to reduce stress and gave them 3 minutes to acclimate. Then, we dropped five crickets of equal size into the arena from out of view behind a curtain. We recorded (i) number of crickets eaten, (ii) number of capture attempts (attacks) and (iii) number of successful attempts in 15 min to calculate a foraging score. We also recorded (iv) handling time measured as the time from the predator attacked the prey to the prey was eaten. The foraging score was calculated as in Michelangeli, Chapple, and Wong (2016):

$$\text{foraging score} = \frac{\text{number of crickets eaten}}{\text{total number of crickets fed}} \times \frac{\text{number of successful attempts}}{\text{total number of capture attempts}}$$

In the analysis of both foraging scores and handling time, five data points were excluded from the analysis because we did not get video recordings for these lizards. In the analysis of handling time, we excluded an additional 13 data points which were lizards (four data points) that did not eat any crickets during the trial and lizards (nine data points) that ate the crickets inside their shelter. We kept data points collected from these lizards in other measurements. The sample size of this experiment was a total of 37 lizards (19 males and 18 females).

2.5 | Thermal preference

Lizards were fasted for 1 day prior to the trial. We set the room temperature at 22°C during the trial, which was the same room temperature as in our animal facility. The thermal gradient had 10 lanes, which were warmed by heating tape (BriskHeat) at one end and a recirculating chiller bath (Haake F3-C, Germany) at the other end. The bottom of each lane was covered with a thin layer (<3 mm) of brick sand as substrate. We insulated the arena with expanded polystyrene foam to minimise temperature fluctuations. We used a black marker pen to designate 14 segments for each lane in the arena.

The thermal gradient ranged from 18.6 to 44.3°C (the two opposite ends, segment 14 and segment 1).

Each lizard was tested twice, with a 4-day interval between measurements. Before the trial, we weighed the lizards with a digital balance (nearest .001 g). At the beginning of each trial, we gently put a focal lizard in the middle of each lane (segment 7). Focal lizards were able to roam freely in the thermal gradient from 08:00 to 16:00, which are the major active hours of these lizards in the wild. From a monitor in the other room, we recorded the position at which the lizard was thermoregulating before we went inside the experiment room to measure body temperature. It was measured using an infrared thermometer (Ryobi RIT310, Victoria, AU) pointed at the lizard's pelvic girdle at a distance within 10 cm. This thermometer's sensor has a distance-to-spot (DS) ratio of 10:1. This meant the sensor measured a spot of 1 cm in diameter on the lizard (mean SVL 4 cm), when the thermometer was 10 cm above the lizard. Care was taken to only measure lizard surface temperature and not substrate temperature. The lizard surface temperature was taken instead of the cloacal temperature because these are such small lizards. Given their small size, we expect only minimal temperature differences between body and skin surface (Chukwuka et al., 2019; Porter et al., 1973). We recorded the substrate temperature using thermocouples (Omega HH912T, USA) right after body temperature measurement. The lizards were able to acclimate for an hour, and hence, the first measurement of body temperature was an hour after the trial commencement. After the first measurement, we measured their body temperature every 20 min for 4 h, resulting in 13 measures per day. This time interval was enough for the lizards to come back to their selected spot in the thermal gradient after disturbance. Following Goulet et al. (2017), we calculated the mean body temperature as their preferred body temperature. One individual was not able to be measured on the second measurement and hence we excluded that data point from this analysis. We kept data points collected from this individual in the first measurement. The sample size of this experiment was a total of 40 lizards (20 males and 20 females).

2.6 | Statistical analysis

We examined the relationship between body condition and parasite infections (both endo- and ectoparasites) by using linear models, where the body condition index was the response variable and endoparasite infection (infected or non-infected) and ectoparasite infection were the two explanatory variables. The body condition index was calculated as the residual of a linear regression between log-transformed body weight and log-transformed SVL, both measured within a day of capture back at the laboratory. We treated the endoparasite infection as a binary measure (no infection represented no egg was found in faecal samples) because parasite load in the faecal sample may not reflect the actual infection intensity in the host (Mehlhorn, 2016). Moreover, our preliminary analysis suggested no continuous relationship between parasite loads (endoparasites or

ectoparasites) and body condition (Figure S1). Thus, we treated both endo- and ectoparasite loads as binary measures in the model.

We tested whether endo- and ectoparasite infections differed between the sexes. We used binomial regression models for endoparasite infection (positive or negative) and ectoparasite load (positive or negative) as the response variable with sexes as the fixed variable.

We used linear mixed models to examine whether endoparasite infection and ectoparasites infestation were related to the whole-organism performance while controlling for the additional fixed effects of body condition index (continuous) and batch (categorical with four levels). We calculated the body condition index for each trial as the residuals of the linear regression between log-transformed body weight, which were measured on the day of each trial, and log-transformed SVL, which were measured on the day of capture. We treated both endoparasites and ectoparasites as binomial variables (whether or not the lizard was parasitised). Lizard ID was included in the models as a random effect to account for between-individual variation. We used the data from all trials instead of averaging or taking the maximum value of the data across different trials. Hence, we included the random effect of trial number to account for within-individual variation among trials (Careau & Wilson, 2017). The data distribution of normality was checked using the Shapiro-Wilk test and a quantile-quantile plot (qqplot). We transformed the data to meet the LMM assumption of normality when necessary (Table 1).

We tested the association between parasite infection and foraging efficiency using foraging scores and handling time as response variable. The total handling time of a lizard depended on the number of crickets eaten in the trial. Therefore, similar to Verwajen et al. (2002), we used the residuals of the regression of log-transformed handling time versus the number of crickets eaten. The same random and fixed effects were used as in previous models, with an additional covariate of cricket weight. Trial number was included as a fixed effect instead of a random effect to avoid overfitting the model. Lizard ID was included as a random effect. We transformed (log+1) the foraging scores to meet model assumptions (Table 1c). The LMM was conducted using the package lme4 (Bates et al., 2015). We calculated the corresponding *p*-values of the fixed effects using Satterthwaite's method with the package lmerTest (Kuznetsova et al., 2017). The *p*-values were adjusted using Bonferroni method due to multiple comparisons of endo- and ectoparasitic effect.

To test for thermal preference, we first used a linear model to investigate whether parasite infections were associated with preferred body temperature in the thermal gradient. As suggested by Camacho and Rusch (2017), body size (continuous), sex (male or female) and batch (categorical with four levels) were included as fixed effects. We excluded lizard ID from the model because the variation of lizard ID as a random factor was close to zero, which lead to singularity of the model (to avoid pseudoreplication, see Supporting Information for the Bayesian model including lizard ID). That meant there was no between-individual variation in thermal preferences

within each fixed effect. We chose to run the model with sacrificial pseudoreplication because dropping a random factor with low variation would not have an effect on the estimates (Schank & Koehnle, 2009). We calculated the powers of each model using the package simr (see Supporting Information for the power analysis; Green & MacLeod, 2016). All statistical analyses and data transformations were conducted in R v4.0.2 (R Core Team, 2020).

3 | RESULTS

Sixty per cent of the lizards hosted at least one species of ascarid parasite (embryonated eggs, 0–4995; Figure S2) and 30% of the lizards harboured trombiculid mites (chigger mites, 0–40; Figure S3). Ascarid parasite load was not related to trombiculid mite load (Figure S4). Body condition was neither related to whether or not lizards were infected with endoparasites ($\beta = .019$, $p = .63$) nor with ectoparasites ($\beta = .052$, $p = .23$). Males and females did not differ in their endoparasite infection ($\beta = .42$, $p = .52$) or mite infection ($\beta = -.48$, $p = .49$). The results of the power analysis showed that our models had a power of over 80% to detect a significant effect when the effect size was large ($>.8$) but a power of 55% when the effect size was small (.3).

3.1 | Sprint speed

The interaction between endoparasite infection and ectoparasite infestation was not related to maximum sprint speed (Figure 2a; Table 1a; $\beta = .46$, $p = .12$). Endoparasite infection was not related to maximum sprint speed ($\beta = -.14$, $p = .84$), but ectoparasite infestation was negatively related to maximum sprint speed ($\beta = -.50$, $p = .027$), meaning that the sprint speed was lower in lizards infected with ectoparasites.

3.2 | Endurance

We did not find a relationship between endurance and body size of lizards (Figure S5). The interaction between endoparasite infection and ectoparasite infestation was not related to endurance (Figure 2b; Table 1b; $\beta = 3.28$, $p = .09$). Likewise, endurance was not related to either endoparasite infection ($\beta = -1.10$, $p = .66$) or ectoparasite infestation ($\beta = -1.84$, $p = .42$). However, male lizards had a significant higher endurance than female lizards ($\beta = 1.83$, $p = .007$).

3.3 | Foraging efficiency

The interaction between endoparasite infection and ectoparasite infestation was not related to either foraging scores (Figure 2c; Table 1c; $\beta = -.01$, $p = .99$) or residual handling time (Figure 2d;

TABLE 1 Outcome of the linear mixed models testing the effect of endoparasites and ectoparasites on (a) sprint speed, (b) endurance, (c) foraging scores and (d) handling time.

Response variable	Fixed term	Estimate	Standard error	Degrees of freedom	t-Value	p-Value
(a) Sprint speed (log-transformed)	Intercept	-.72	.13	32.53	-5.61	<.001
	Body condition index	2.54	2.37	77.17	1.07	.29
	Sex (male)	.04	.09	32.00	.47	.64
	Batch (2)	.08	.12	32.00	.65	.52
	Batch (3)	.10	.19	32.00	.52	.60
	Batch (4)	-.11	.15	32.00	-.75	.46
	Endoparasite (infected)	-.14	.13	32.00	-1.09	.84
	Ectoparasite (infected)	-.50	.18	32.00	-2.77	.027
	Endo-xectoparasite	.46	.22	32.00	2.10	.12
(b) Endurance (square-root-transformed)	Intercept	9.58	1.06	13.17	9.06	<.001
	Body condition index	-3.08	14.12	74.47	-.22	.83
	Sex (male)	1.83	.64	32.03	2.86	.007
	Batch (2)	-.24	.84	32.28	-.28	.78
	Batch (3)	-.38	1.29	31.85	-.30	.77
	Batch (4)	-1.30	1.04	31.89	-1.25	.22
	Endoparasite (infected)	-1.10	.87	31.93	-1.26	.66
	Ectoparasite (infected)	-1.84	1.23	32.26	-1.50	.42
	Endo-xectoparasite	3.28	1.49	32.22	2.20	.09
(c) Foraging score + 1 (log-transformed)	Intercept	.08	.54	40.92	.15	.88
	Body condition index	-.57	.76	36.00	-.76	.45
	Sex (male)	.08	.05	30.59	1.62	.12
	Batch (2)	.06	.06	31.22	.92	.36
	Batch (3)	.10	.10	35.00	.99	.33
	Batch (4)	-.03	.08	33.35	-.33	.75
	Cricket weight	.74	3.10	39.84	.24	.81
	Trial number	.06	.03	35.42	1.88	.07
	Endoparasite (infected)	.02	.06	29.50	.34	.99
	Ectoparasite (infected)	.03	.10	29.89	.27	.99
	Endo-xectoparasite	-.01	.12	30.55	-.07	.99
(d) Handling time (residual)	Intercept	.456	.914	51.00	.50	.62
	Body condition index	-.740	1.296	51.00	-.57	.57
	Sex (male)	.002	.059	51.00	.03	.98
	Batch (2)	.003	.079	51.00	.03	.98
	Batch (3)	.101	.131	51.00	.03	.98
	Batch (4)	.103	.110	51.00	.94	.35
	Cricket weight	-2.978	5.244	51.00	-.57	.57
	Trial number	-.005	.059	51.00	-.08	.94
	Endoparasite (infected)	.048	.085	51.00	.56	.99
	Ectoparasite (infected)	-.066	.115	51.00	-.57	.99
	Endo-xectoparasite	-.104	.147	51.00	-.71	.99

Note: All reported *p*-values are adjusted using Bonferroni method. The significance level was set as 0.05. All bold values present are the *p*-values adjusted using Bonferroni method.

Table 1d; $\beta = -.104$, $p = .99$). Foraging scores were not related to either endoparasite infection ($\beta = .02$, $p = .99$) or mite infestation ($\beta = .03$, $p = .99$). We found the same result from the model of

residual handling time that endoparasite infection ($\beta = .048$, $p = .99$) and ectoparasite infestation ($\beta = -.066$, $p = .99$) did not have a significant relationship with foraging efficiency.

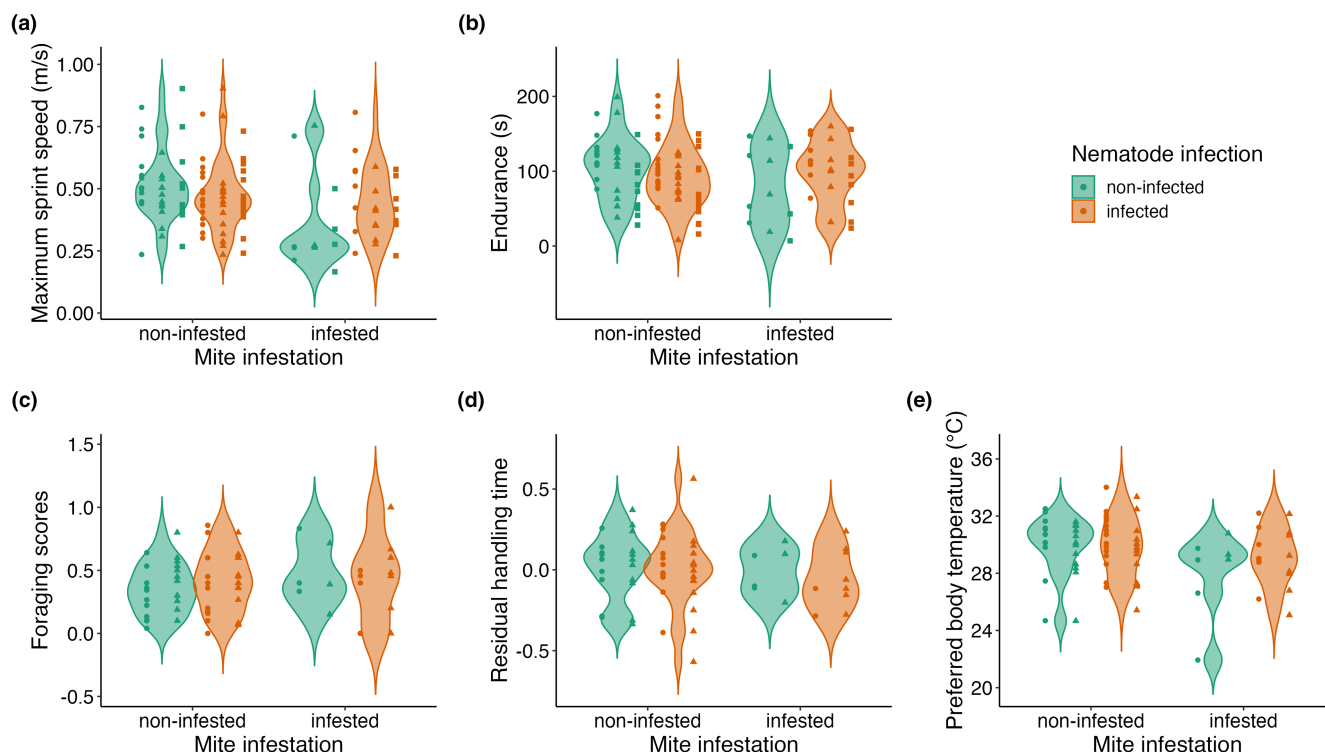


FIGURE 2 Maximum sprint speed (a), endurance (b), foraging scores (c), residual handling time (d) and preferred body temperature (e) as a function of infection status (nematodes or mites). The figure depicts two groups of lizards. On the left are lizards with no mites while on the right are mite-infested lizards. Both groups either have nematodes or are uninfected with nematodes. Shapes of the point represent the three repeated measurements (● = 1, ▲ = 2, ■ = 3).

Response variable	Fixed term	Estimate	Standard error	t-Value	p-Value
Preferred body temperature (square-transformed)	Intercept	873.34	281.92	3.10	.003
	Sex (male)	-32.41	31.80	-1.02	.31
	SVL	2.25	6.83	.33	.74
	Batch (2)	-51.24	41.39	-1.24	.22
	Batch (3)	-40.30	62.15	-.65	.52
	Batch (4)	-37.36	49.67	-.75	.45
	Trial number	-39.36	28.11	-1.40	.17
	Endoparasite (infected)	-4.14	42.21	-.10	.99
	Ectoparasite (infected)	-93.46	60.54	-1.54	.39
	Endo-xectoparasite	48.11	73.20	.66	.99

Note: The significance level was set as 0.05. All bold values present are the *p*-values adjusted using Bonferroni method.

TABLE 2 Outcome of linear model testing the effect of endoparasites and ectoparasites on preferred body temperature (°C).

3.4 | Thermal preference

The linear model showed that preferred body temperature was not related to the interaction between endo- and ectoparasite infection (Figure 2e; Table 2; $\beta = 48.11$, $p = .99$). Preferred body temperature was not related to either endoparasite infection ($\beta = -4.14$, $p = .99$) or ectoparasite infestation ($\beta = -93.46$, $p = .39$).

4 | DISCUSSION

We found that having mites was negatively related to sprint speed while having nematodes was not related to any metric of whole-organism performance we measured. Furthermore, body condition was unaffected by parasite infection. Together, this suggests that although mites negatively affect host sprint speed, this effect did not

translate into reduced body condition. Hence, the cost of parasite infection was negligible. Garden skinks can be found in urban areas while also inhabiting natural bushland (Wilson & Swan, 2017). Reptiles can benefit from urbanised areas where they can gain access to better, or more resources and grow larger in body size (Putman & Tippie, 2020). Our lizards were collected in urban areas so individuals in our study population may be, on average, in better body condition than populations in other habitats (STRANGE framework; Webster & Rutz, 2020). Parasites did not affect body condition, in our observed condition range. However, whether this is also the case for individuals at even lower body conditions than our lizards, remains to be investigated.

In our study, ecto- and endoparasites were not related to whole-organism performance capacity, except for the negative relationship between ectoparasitic mites and sprint speed. Although many studies have found a negative relationship between host performance and parasite load (Finnerty et al., 2017; Hicks et al., 2018; Maia-Carneiro et al., 2018), an evolutionary arms race may lead to a coexistence of the host and parasite (Koskella, 2018), and hence, a benign host-parasite relationship (Binning et al., 2014; Hahn et al., 2018; Taggart et al., 2018). Our results showed no relationship between nematodes and the performance of lizards. Similar results were also reported for the keelback snake (*Tropidonophis mairii*; Mayer et al., 2015), which found no relationship of gastrointestinal nematode infection with locomotion. In contrast, we did find a negative relationship of sprint speed and mite infestation (measured as present/absent). However, there was no effect when mite infestation was measured as continuous variable, indicating that the effect size did not scale with the number of mites on the lizard (Table S1). For example, in Mesoamerican cane toads (*Rhinella horribilis*; Kelehear et al., 2019), locomotion was negatively affected by lung nematode infection. In the case of lizards, sprint speed is important when foraging and for escaping from predators (Landry Yuan et al., 2021; Pagan et al., 2012). Garden skinks are ground-dwelling species preyed upon by a range of elapid snakes (Richard Shine, 1995). A reduction in sprint speed may constrain their ability to escape an actively foraging predator (Downes & Shine, 2001). However, endurance, which is indicative of social dominance (Perry et al., 2004; Robson & Miles, 2000), was not related to parasite infections. In our study, males had significantly greater endurance than females while both are morphologically similar and do not differ body length or head length (Simbotwe, 1985). The better endurance capacity may be beneficial for males to maintain a territory in the breeding season (Torr & Shine, 1996). This result is consistent with the findings in other reptiles, in which males generally have a better performance than females (Noble, Fanson, & Whiting, 2014; Qi et al., 2014).

Alternatively, many trophically transmitted parasites can manipulate host behaviour to maximise their transmission rate (Binning et al., 2017; Parker et al., 2015; Poulin & Maure, 2015). A conflict between different parasites may result in no detectable parasitic effect in hosts having multiple parasite infections (Hafer & Milinski, 2016). For example, an acanthocephalan parasite (*Polymorphus minutus*) alters the habitat preference of amphipods (*Gammarus roeseli*) to increase their probability of being predated but this manipulation can be interrupted by the co-infection of a microsporidia parasite, resulting in an absence of any difference in habitat preference between infected and

non-infected individuals (Haine et al., 2005). This parasite-parasite relationship may explain why we found no reduction in sprint speed in lizards that were parasitised by both mites and gastrointestinal worms. Parasitic larvae of chigger mites infect host lizards when they move across a contaminated patch. Once the larvae are fully fed, they drop to the ground and complete their free-living life cycle (including mating and reproducing) in the soil. In contrast, ascarid parasites live and reproduce in the intestine of host lizards. The infective stage is then released into the environment with the faeces. The gastrointestinal worms may not alter the host performance or can even enhance the performance in some cases until the worms reach the infective stage (Dianne et al., 2011; Weinreich et al., 2012). However, we did find parasite eggs in the faeces, suggesting that the gastrointestinal worms were producing infective stages. The life cycle of this gastrointestinal worm is still unknown. For the possible endoparasite species (*Baerietta hickmani*, *Maxvachonia chabaudi* and *Skrjabinodon* sp.), the garden skink is the definitive host of the gastrointestinal worm and the survival of the lizards is necessary for the parasite transmission. Thus, natural selection could favour gastrointestinal worms that maintain host performance and not reduce it (Weinersmith & Earley, 2016).

Host behavioural responses also play an important role in the arms race between hosts and parasites. Therefore, we predicted parasitised individuals would use behavioural fever to help combat parasitism. However, we did not find any evidence of behavioural fever in parasitised lizards—lizards did not seek out warmer temperatures in a thermal gradient. Alternatively, animals may bask in the sun when infected to expose ectoparasites to UV light (Bush & Clayton, 2018), and not to increase their own body temperature. In our study, the heat source came from the ground and basking behaviour only reflects temperature preference. Given the weak relationship between parasites and whole-organism performance in our study, parasitised lizards likely did not need to raise their body temperature or may not need to particularly seek out a sunny spot to compensate for parasitism. In addition, hosts that elevate their body temperature may compromise other physiological responses (Gangloff & Telemeco, 2018), such as increased oxygen consumption (Gangloff et al., 2016). Moreover, some parasites have a better growth rate in warmer environments, which may favour the parasite (Dube et al., 2018; Macnab & Barber, 2012). Thus, parasitised individuals sometimes avoid environments that benefit the parasite when the cost of parasitism is greater than the disadvantage of suboptimal performance capacity (Megía-Palma et al., 2020; Oppliger et al., 1996). Under these circumstances, seeking out a cool environment (behavioural chill) can be beneficial for the host when it has already been parasitised (Klemme et al., 2021).

The behavioural change may also be a consequence of parasite manipulation because parasites can reduce the thermal tolerance of their host (Sherman, 2008). Behavioural fever can increase immunity and decrease the performance of parasites. To sabotage this protective behaviour, parasites may increase host heat sensitivity and discourage the host from seeking a warmer environment (Greenspan et al., 2017). External temperature can determine the physiology and performance capacity of ectothermic animals (Beltrán et al., 2020; Goulet et al., 2017). Consequently, the alteration of thermal tolerance may limit animal distributions (Doody & Moore, 2010;

Gutiérrez-Pesquera et al., 2016; Sunday et al., 2011), reduce breeding opportunities (Alonso et al., 2015) and ultimately decrease survival rate (Hall & Warner, 2019). One way to disentangle behavioural chill and parasitic manipulation is to use an experiment such as injecting lipopolysaccharide (LPS; Deen & Hutchison, 2001; Goessling et al., 2017; Merchant et al., 2008) or experimental infection with parasites (Karavlan & Venesky, 2016; Sauer et al., 2019). Individuals may also exhibit behavioural fever directly at the time of infection. Since we did not know how long the lizards had been infected with parasites, this may have made it harder to detect a potential effect. A manipulation experiment on the parasite infections would provide a better picture of using behavioural fever as a defence against parasites.

In conclusion, garden skinks, a lizard that thrives in urban areas, appears to largely cope with parasitism. We only found a negative relationship between mites and sprint speed, and no relationship with endurance or foraging efficiency. At the same time, when gastrointestinal worms were present with mites, we did not detect any significant relationship of mites with whole-organism performance capacity or foraging efficiency. Our power analysis indicated that the sample size of our study may have been inadequate to detect smaller effect sizes but our results showed large effect sizes in sprint speed, endurance and thermal preference models. These findings suggest that future studies should use a larger sample size to increase the statistical power in the foraging efficiency model. Mite-infested lizards did not select a higher body temperature and the variation explained by infestation is generally low. Therefore, we conclude that there is no strong evidence of a relationship between parasites and thermoregulation. Taken together, this study suggests that this short-lived lizard copes with its parasites without an apparent behavioural defence.

AUTHOR CONTRIBUTIONS

Ko-Huan Lee: Conceptualization; methodology; data curation; investigation; formal analysis; visualization; project administration; writing – original draft; writing – review and editing; funding acquisition; validation; software. **Martin J. Whiting:** Conceptualization; methodology; funding acquisition; supervision; writing – review and editing; resources. **Stephan T. Leu:** Conceptualization; methodology; funding acquisition; writing – review and editing; supervision.

ACKNOWLEDGMENTS

We thank Levi Brown, Rou-Chia Huang, Samuel Brennan and Samantha Richardson for helping collect lizards, husbandry, conduct behavioural trials, and score footage of lizard behaviours. We are grateful to Rou-Chia Huang for providing her drawing of lizards in the graphical abstract. We also appreciate the assistance provided by the animal technicians of the fauna park of Macquarie University. Open access publishing facilitated by Macquarie University, as part of the Wiley - Macquarie University agreement via the Council of Australian University Librarians.

FUNDING INFORMATION

This research was supported by HDR budget of Macquarie University. KHL was supported by an international Macquarie

University Research Excellence Scholarship (iMQRES) and a Taiwanese Government Scholarship for Overseas Study.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data are available at OSF: https://osf.io/r45gd/?view_only=2fa60c60960f42a5b4a4122e9dbdc678.

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How to cite this article: Lee, K.-H., Whiting, M. J., & Leu, S. T. (2023). Are whole-organism performance and thermal preference linked to endo- and ectoparasites in a short-lived lizard? *Ethology*, 129, 432–443. <https://doi.org/10.1111/eth.13379>