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The fast-food effect: costs of being a generalist in a humandominated landscape

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The *fast-food effect*: costs of being a generalist in a human-dominated landscape.

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19 Abstract

- 20 Agricultural expansion in Southeast Asia has converted most natural landscapes into mosaics of
- 21 forest interspersed with plantations, dominated by the presence of generalist species that benefit
- 22 from resource predictability. Dietary shifts, however, can result in metabolic alterations and the

23 exposure of new parasites that can impact animal fitness and population survival. Our study 24 focuses on the Asian water monitor lizard (Varanus salvator), one of the largest predators in the 25 Asian wetlands, as a model species to understand the health consequences of living in a human-26 dominated landscape in Sabah, Malaysian Borneo. We evaluated the effects of dietary diversity 27 on the metabolism of monitor lizards and the impact on the composition of their parasite 28 communities in an oil palm-dominated landscape. Our results showed that (1) rodent-dominated 29 diets were associated with high levels of lipids, proteins, and electrolytes, akin to a *fast-food* 30 based diet of little representativeness of the full nutritional requirements, but highly available, 31 and (2) lizards feeding on diverse diets hosted more diverse parasite communities, however at 32 overall lower parasite prevalence. Furthermore, we observed that the effect of diet on lipid 33 concentration differed depending on the size of individual home ranges, suggesting that 34 sedentarism plays an important role in the accumulation of cholesterol and triglycerides. Parasite 35 communities were also affected by a homogeneous dietary behavior, as well as by habitat type. 36 Dietary diversity had a negative effect on both parasite richness and prevalence in plantations, 37 but not in forested areas. Our study indicates that human-dominated landscapes can pose a 38 negative effect on generalist species and hints to the unforeseen health consequences for more 39 vulnerable taxa using the same landscapes. Thus, it highlights the potential role of such a widely 40 distributed generalist as model species to monitor physiological effects in the ecosystem in an oil 41 palm-dominated landscape.

42 Keywords

43 Asian water monitor lizard, Borneo, oil palm, diet, animal health, parasites, blood chemistry.

44 Introduction

45	Agricultural expansion in the tropics has converted most natural landscapes into mosaics of
46	forest and industrialized crops, altering the availability and distribution of food resources for a
47	wide range of wildlife (Oro et al., 2013). While for some taxa deforestation and land use change
48	can result in resource depletion, for others, anthropogenic changes in the landscapes offer an
49	abundant food source with human-base resources that are both abundant and predictable
50	(McKinney, 2006; Newsome et al., 2014). As a result, many wildlife species have adapted to
51	benefit from these resources, leading to larger populations that are more aggregated and better
52	fed (Prange et al., 2003). Raccoons (Procyon lotor), for example, have been reported to have
53	higher population densities and survival rates in urban and suburban areas in Northern U.S. and
54	Canada, as well as very low weight loss during winter, compared to those living in more natural
55	environments (Hoffmann, 1979; Rosatte et al., 1991; Prange et al., 2003). Moreover, shifts in
56	intra- and inter-species interactions are more likely to be observed in human-modified landscapes
57	(Ciucci et al., 2020), including an increased risk of human-wildlife contact (Hopkins et al.,
58	2014), favouring changes in pathogen host range and distribution (Patz et al., 2000; Gillespie and
59	Chapman 2006; Lafferty et al., 2006; Cardoso et al., 2016; Bonell et al., 2018).
60	In Asia, one of the largest beneficiaries of anthropogenic food is the Asian water monitor lizard
61	(Varanus salvator), one of the largest predators in the region's wetlands (Traeholt, 1994;
62	Guerrero-Sanchez, 2021). The species natural habitat is linked to lowland freshwater, such as
63	mangroves, swamps, and wetlands under 1000 meters above the sea level (m.a.s.l; Horn and

64	Gaulke, 2004), where they feed on a large range of animals, such as fish, frogs, invertebrates,
65	birds, small mammals, as well as animal carcases (Traeholt, 1994; Uyeda, 2009). Nonetheless,
66	monitor lizards are exceptionally persistent in anthropogenic habitats, being particularly
67	abundant in the proximity of farms, households, and urban areas (Uyeda, 2009; Karunarathna et
68	al., 2017). High food availability, as well as reduced areas of suitable habitat for the species, has
69	driven lizards inhabiting oil palm habitats to a sedentary behavior, establishing home ranges that
70	are significantly smaller than those of lizards living in natural forest (Guerrero-Sanchez et al.,
71	2022). Consequently, these adaptations to agricultural landscapes have induced changes in their
72	ecology and behavior, altering their physiology through a higher accumulation of blood
73	metabolites and exposure to novel parasite assemblages (Jessop et al., 2012; Smyth et al., 2014).
74	Dietary shifts induced by human-modified habitats have physiological consequences for wildlife
75	health, as they often provide resources that may vary considerably in terms of quality, energy,
76	and nutrient composition from natural diets (Oro et al., 2013). For example, body condition can
77	increase as a result of a higher and predictable intake of calories (Kaneko and Maruyama, 2005),
78	or decrease if anthropogenic food is low quality (Liker et al., 2008). Anthropogenic food can
79	boost wildlife body condition and increase immune defences, as shown in lace monitors (V.
80	varius) foraging on human subsidies in Australia, where provisioned individuals were not only
81	larger and heavier than non-provisioned animals, but they also showed lower intensity of blood
82	parasites (Jessop et al., 2012). By being localized, anthropogenic food can also reduce wildlife
83	movement and foraging time (Murray et al., 2015), which could be compared to the accessible
84	and affordable fast-food for humans. Just like fast-food has consequences to human health

85	(Davis and Carpenter, 2009), shifts to a more homogeneous and highly caloric diet also have
86	physiological implications in animals. Lace monitors feeding on human subsidies have reported
87	higher levels of creatinine kinase (CK) and aspartate aminotransferase (AST) compared to those
88	feeding on more natural diets (Jessop et al., 2012).
89	Parasite diversity, on the other hand, is strongly linked to the host dietary behavior (Lafferty,
90	1999; Poulin and Morand, 2004). Thieltges and Poulin (2016), for example, found that the prey
91	range in birds at the Pacific coast of U.S. and Mexico, is positively associated to parasite
92	richness, where birds with broader diets showed a higher parasite richness. Host susceptibility to
93	infection and higher parasite loads can also be the consequence of a poor-quality diet (Ezenwa,
94	2004). For example, rock iguanas (Cyclura cychlura) supplementary fed with processed food,
95	rich in carbohydrates and sugar, not only presented an altered nutritional status, but they showed
96	an increased prevalence of hookworm (Knapp et al., 2013). In other species, the induced
97	sedentary behavior, reflected in the reduction of the individual home range and population
98	aggregation, increases exposure to infected conspecifics, as well as the shedding and
99	accumulation of pathogens into the environment (Becker and Hall, 2014; Gilbert et al., 2016).
100	Here, we evaluated the influence of dietary diversity on the physiological responses and
101	exposure to parasites of Asian water monitor lizards in an oil palm-dominated landscape. By
102	providing reliable food resources, oil palm (<i>Elaeis guineensis</i>) plantations could boost the body
103	condition of lizards, increase their immune defences, and reduce their foraging time, which in
104	turn could reduce parasite fitness by decreasing individual susceptibility to infection and
105	promoting quick recovery (Becker et al., 2015). We hypothesized that the feeding behavior of

plantation lizards was less diverse than that of lizards living in the forest, and that this tendency
would be reflected in (1) higher values of biochemical markers associated with shifts in the
dietary diversity, and (2) a reduction in overall parasite diversity and increased parasite
prevalence. Using *V. salvator* as model species, we aim to contribute to the understanding of the
physiological implications of species adaptations to human-dominated landscapes, and provide
information that can be extrapolated to other, more cryptic, and vulnerable species.

112 Materials and methods

113 Study area

The study was conducted in the Kinabatangan floodplain (5°10' - 5°50'N; 117°40' - 118°30'E), 114 115 located in the east coast of Sabah (Malaysian Borneo; Figure 1). The floodplain (~30 m.a.s.l.) 116 consists of a complex matrix of different types of forest interspersed with rural settlements and 117 large extensions of oil palm crops along the Kinabatangan River, which, along with oxbow lakes 118 and tributaries, irrigate the landscape either seasonally or permanently (Estes et al., 2012). Along 119 the Kinabatangan River, the Lower Kinabatangan Wildlife Sanctuary (LKWS) expands in a 120 series of patches of protected forest (hereafter referred to as "lots") encroached between the main 121 river and industrial palm oil. Connectivity among these lots, and between lots and other forested 122 areas, is generally poor, often consisting in narrow strips of highly degraded forest, and in the 123 worst cases, completely absent (Ancrenaz et al., 2004; Abram et al., 2014).

124 Animal sampling

125 We spent a total of 3,055 trap/days between October 2013 and September 2016, split in three 126 forest lots (Lot 5, 6, and 7) within the LKWS and three surrounding oil palm plantation estates 127 (Hillco, Kopi and Kuril; Figure 1). We established two transects in each site and placed one cage 128 trap every 400 meters for a total of five traps per transect (Guerrero-Sanchez et al., 2021). Traps 129 were then opened and baited in the early morning, using chicken entrails, and checked in the 130 early afternoon. Asian water monitor lizards were grouped by habitat (forest/plantation) and site 131 (forest lot/plantation estate), according to where they were trapped. Since monitor lizards, 132 especially those living in the boundaries, can roam in both types of habitats, using oil palm 133 plantations as food sources and forested areas as a shelter (Guerrero-Sanchez et al., 2021), we 134 established a third group for those that were captured in both types of habitats to avoid bias or 135 pseudo-replications. All trapped lizards were tagged with an intradermal transponder (ID-1AA; 136 Trovan LTD, UK).

137 Each lizard was weighted, and body length was measured from the tip of the mouth to the cloaca 138 (snout to vent length [SVL]). We also collected up to 2 ml of blood from the coccygeal vein for 139 the biochemical analysis, which included lipids, proteins, and electrolytes. Although it is safe to 140 collect up to 5% of blood in relation to body weight (Jacobson, 1993), to minimize the risk of 141 lesions caused by the venepuncture (*i.e.*, accidental pinch of the caudal nerves or rupture of the 142 vein), we only collected blood from individuals over 3 kilograms. Due to difficulties in sex 143 determination by physical methods, not all individuals were sexed unequivocally. Frynta et al. 144 (2010) reported that male varanids are three times larger than females. Therefore, by being

- 145 unable to determine the sex of all individuals, we could not estimate their age range, and we
- 146 omitted sex and age as independent variables in the analysis.

147 **Diet inventory**

148 As a proxy to describing the dietary diversity of monitor lizards in the study site, we recorded an 149 inventory of stomach contents of all trapped lizards. Regurgitation is a common response 150 mechanism to threatening situations (*e.g.*, being trapped) in reptiles (Greene, 1988), and thus, it 151 was anticipated to happen in most (if not all) of the trapped individuals during the study. The 152 regurgitated content was collected, and food items were identified and classified into taxonomic 153 groups, according to morphological features. The food items recorded in this study only 154 represent what captured individuals ate prior to being captured and are likely informative of local 155 food availability rather than dietary preferences. We used the term "dietary diversity" instead of 156 "prey diversity" to avoid any confusion with individual preferences.

157 Biochemical analysis

Blood samples were processed within 2 hours of collection and the serum was separated from
blood cells through centrifugation (1,000 x *G* for 10 min) and kept at -20 °C until analysis
(Fudge, 2000). Samples were analyzed for a full biochemistry panel in a commercial laboratory
(Gribbles Sdn. Bhd, Sandakan, Malaysia). For this study, we selected a set of biochemical
elements (hereafter *biomarkers*) commonly associated with dietary behavior. Cholesterol
(including low- and high-density lipoproteins) and triglycerides are indicators of energy intake,

164 use, and storage in an individual. They are also commonly associated with highly caloric food 165 and, together with sedentary behavior, drivers of cardio-vascular diseases (Meyer and Harvey, 166 2004). Proteins are a significant part of an individual's metabolism, as they are fundamental for 167 body structure and functionality. Low quality proteins may be reflected in the ability of an 168 animal to perform its biological functions and make it more vulnerable to both metabolic and 169 infectious diseases (Meyer and Harvey, 2004). Uric acid serves as an indicator of protein 170 metabolism, usually of concern when there is an exceedingly high intake of proteins (Meyer and 171 Harvey, 2004). Electrolytes, such as sodium, potassium, and chloride, are essential in tissue 172 homeostasis and strongly related to muscular functionality (Meyer and Harvey, 2004). They are 173 also associated with a high consumption of processed food, as they are a main component of 174 artificial flavoring and preservatives (Meyer and Harvey, 2004).

175 Parasite sampling and identification

176 A cleaned plastic tarp was placed under each trap to collect faecal samples and avoid 177 contamination with free-living nematodes. All faecal samples were processed using a modified 178 formalin-ethyl acetate sedimentation protocol to concentrate parasite eggs, and then samples 179 were examined with a sequential sedimentation-flotation procedure (Frias et al., 2021). We 180 evaluated two measures of parasite infection influenced by dietary diversity: (i) parasite species 181 richness, calculated as the number of parasite taxonomic groups identified in an individual, and 182 (ii) parasite prevalence, expressed as the percentage of individuals positive for a given parasite 183 taxonomic group (Bush et al., 1997).

184 Statistical analysis

185	Dietary diversity was estimated for each sampling site using the Shannon-Wiener diversity Index
186	(H'). Differences between sites and habitats were calculated by analysis of their variance
187	(ANOVA). Body condition, <i>i.e.</i> , an index that reflects the physiological and nutritional status of
188	an individual (Labocha et al., 2014), was estimated as the linear regression between log-
189	transformed body weight and log-transformed body length (Green, 2001).
190	Differences for each biomarker were assessed with generalized linear models (GLM), using two
191	different categorical variables, i.e., habitat (forest v. oil palm plantation), and sites (3 forest lots
192	and 3 oil palm estates). Later, we grouped the study sites according with the habitat type and
193	evaluate the differences within each group. Each biomarker GLM was set with the corresponding
194	family distribution error. GLM models were carried out with the stats v3.6.3 package for R (R
195	Core Team) and validated using the diagnostics for hierarchical regression models (DHARMa,
196	v.0.4.6; Hartig, 2022). Distribution for both biochemicals markers, and parasite data, was
197	assessed using the fitdistrplus v1.1.8 package for R (R Core Team; Delignette-Muller and
198	Dutang, 2015), and are presented in the section 2 of the supplementary material (Fit of
199	distribution for the biochemical values, body condition, and parasite data, by maximum
200	likelihood estimation).
201	To determine if dietary diversity accounted for a significant proportion of the variation between
202	habitats and among sites for each of the biomarkers assessed, generalized estimation equations
203	(GEE) were run by using the geeglm function in geepack v.1.3-1 (Halekoh et al., 2006). Contrary

204	to other generalized linear models that estimate a within-group variance component, GEE
205	models estimate the average response of each group, considering the most suitable between-
206	group correlation structures (Liang and Zeger, 1986; Yan and Fine, 2004; Zuur et al., 2009).
207	Correlation structure were set either as exchangeable or unstructured, while the distribution
208	family error was defined properly for each markers' distribution. All the GEE models in this
209	study were validated with the Pearson correlation test of the residuals.
210	Since sedentarism is a complementary variable to dietary behavior in the metabolism of energy,
211	we use lizards' home range as a proxy to activity pattern. A subset of 10 individuals between 15
212	and 20 kg (presumed adult males), was extracted from the whole sampled population to
213	understand the effect of home range size over the association between dietary diversity and the
214	value of the biochemical markers. Those lizards belonged to a group of 14 individuals tagged
215	with GPS trackers, and which home ranges were defined in a previous study using Local Convex
216	Hull (Guerrero-Sanchez et al., 2022), and all of them were tested for total cholesterol, nine for
217	proteins and electrolytes, and eight for triglycerides, low- and high-density lipoproteins
218	cholesterol. In this case, GEE models were set with either an independent or exchangeable
219	correlation structure and, like in the analysis mentioned above, a proper distribution error was set
220	for each biomarker. Here, the models were also validated with the Pearson correlation of the
221	residuals.
222	Parasite richness and prevalence were estimated per site and habitat type, although only

223 prevalence was compared per habitat type and per site using GLM with Poisson distribution

errors. Prevalence among habitats and sites were also compared per each one of the parasitic

groups with major presence in the study. The effect of dietary diversity and body condition on both parasite richness and prevalence was evaluated with GEE models. In the case of prevalence, models were performed with the overall parasite community and finally, for each one of the parasitic groups with major presence in the study. All models were set with a Poisson error distribution and exchangeable autocorrelation structure. Models were evaluated using the Pearson test of the residuals.

231 **Results**

We captured and marked 402 unique individuals during the study period (3,055 trap/days). Capture data showed that individuals were re-captured within the same transect as in the first time, and none of the individuals were caught in both oil palm plantation and forest. Thus, lizards were grouped only in two categories (forest and oil palm plantation). Data on blood metabolites were available for 256 individuals, and only 73 faecal samples were collected and suitable for the study.

238 **Diet**

The dietary inventory was established based on the stomach content of 132 individuals, and it included 182 prey items categorized into 14 taxonomic groups. The remaining 124 individuals were discarded since they did not vomit or only vomited the bait. Overall, dietary diversity was significantly higher in forest lots than in oil palm plantation (H'_{Forest} = 2.114 v. H'_{Plantation}= 1.052; F = 9309; p < 0.001). Invertebrates such as crabs, centipedes, and woodlice, made up an important part of the diet of lizards in forested areas (54% of the records), while rodents were the
dominant prey in plantations (Table 1 and Figure 2). Fish were almost exclusively represented by
a catfish species from the genus *Pterygoplichthys*, invasive to Borneo and Southeast Asia.

247 Body condition

248 Overall, lizards in oil palm plantations (OPP) had a slightly higher body condition (BC) than

those living in the forest ($BC_{OPP} = 0.389 \pm 0.12$; $BC_{Forest} = 0.353 \pm 0.15$). Among forest lizards,

those captured in Lot 5 (BC_{Lot5} = 0.391 ± 0.13), where the trapping site was placed less than 700

- 251 meters from the plantation boundaries, had a slightly higher body condition than those captured
- in sites placed farther than 700 metres from the plantation boundaries (BC_{Lot6} = 0.337 ± 0.17 ;
- 253 $BC_{Lot7} = 0.345 \pm 0.13$). However, we did not find significant differences among habitats or
- among sites (Supplementary Tables 1 and 2).

255 Biomarkers

256 Lizards inhabiting forested areas presented significantly higher levels of total cholesterol (Forest

257 = 2.04mmol/L v. OPP = 1.8 mmol/L), while lizards in oil palm plantations presented higher

- levels of total proteins (OPP = 80.3 g/L, Forest = 76.6 g/L), and globulin (OPP = 54.1 g/L, Forest
- 259 = 51.1 g/L; Table 1). We also found significant differences among all the sites for total
- 260 cholesterol, low-density cholesterol, high-density cholesterol, total proteins, and albumin.
- 261 However, when we compared sites grouped per type of habitat, only high-density cholesterol
- 262 levels were different among forested sites, while the rest of the markers did not show significant

variations. Oil palm plantation sites, on the contrary, presented significant differences among
them for total cholesterol, low-density cholesterol, total proteins, and albumin (Table 2. See also
Supplementary Tables 1 and 2).

266 The influence of habitat type and home range size

The results of the generalised estimation equation models showed that dietary diversity had a significant negative effect on low- and high-density cholesterol (LDL-Ch, HDL-Ch) in monitor lizards, but that this effect was stronger in plantation areas (Figure 3b and Table 2. See also Supplementary Table 3). Total proteins, on the other hand, increased with dietary diversity, and the association was stronger in oil palm plantations than in forested areas. Triglycerides and potassium showed significantly higher levels associated with low dietary diversity in oil palm plantations, but not in forested areas.

274 For those samples with a known home range size, the intensity of the effect of dietary diversity 275 on body condition and three fat-related biomarkers showed to be dependent on home range size 276 (Figure 3c and 4. See also Table 2 and Supplementary Table 4). Body condition decreased with 277 higher dietary diversity in individuals with large home ranges. However, when home ranges 278 shrank, this correlation gradually shifted tendencies, with body condition increasing along with 279 dietary diversity. Reduction of home range size also boosted a negative association between low 280 density cholesterol dietary diversity. High density lipoprotein cholesterol and triglycerides were 281 higher in individuals with smaller home ranges and lower dietary diversity, but the intensity and 282 direction of the effect shifted gradually from negative to positive with increasing home range 283 sizes.

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284 Parasite species richness and prevalence

285 Faecal samples were collected from 73 lizards ($n_{\text{Forest}} = 32$; $n_{\text{Plantation}} = 41$), and overall parasite 286 prevalence was estimated at 79.4% (n = 58). During our trapping period, conditions surrounding 287 Kuril estate were inadequate for faecal sample collection, *i.e.*, there was an excess of mud due to 288 continuous rain and flooding, and thus, data from this study site were not included in the 289 analysis. A total of 10 parasite taxonomic groups were identified, corresponding to nematodes (N 290 = 8), cestodes (N = 1) and trematodes (N = 1; Table 3). Nematodes included parasites from the 291 genus Capillaria (42.4%), Strongyloides (17.8%), Trichuris (9.5%), Physaloptera (5.4%) and 292 Ascaris (1.3%), and from the orders Oxyurida (35.6%), Strongylida (26%) and Spirurida (5.4%). 293 Out of the 10 taxonomic groups of helminths identified, all of them were found in forest, while 294 only eight were detected in oil palm plantations, where Ascaris spp. and Trematoda were absent. 295 Parasite prevalence, on the other hand, was significantly higher in plantation estates than in 296 forest sites (Table 2). We also found significant differences among sites, where Hillco estate 297 showed the highest parasite prevalence (83%) among the study sites, followed by Kopi estate 298 and Lot 5 (80%), and Lot 6 (71.4%). Forest lizards showed a significantly higher prevalence of 299 Trichuris (15.6% v. 4.8% in oil palm plantation), spirurids (9.37% v. 2.44%), and oxyurids 300 (43.8% v. 29.3%), while plantation lizards had a significantly higher prevalence of parasites of 301 the genus Strongyloides (22% v. 12.5). Cestodes were only found in two individuals, one in Lot 302 7 and in one in Hillco estate, while parasites of the genus *Ascaris* spp. were found only in Lot 7. 303 Trematodes, on the hand, were only found in three individuals in Lot 6.

304	Positive association between parasite richness and body condition was observed in oil palm
305	plantation sites, but not in forested areas (Table 2). No association between body condition and
306	prevalence was found neither in forest nor oil palm plantation Ssupplementary table 5). For
307	specific parasites, the prevalence of <i>Trichuris</i> was higher in areas of high dietary diversity, while
308	the prevalence of <i>Physaloptera</i> and <i>Strongyloides</i> was higher in areas with less diverse diet
309	(Table 2 and Supplementary table 5).
• • •	
310	Regarding the effect of habitat on the parasite community associated with the monitor lizards, we
311	found that dietary diversity had a significant effect on both parasite richness and prevalence, and
312	this effect is different according to the type of habitat. While in the forest, sites with more
313	heterogeneous diet shows a positive tendency in such associations, they become negative in oil

314 palm plantation (Figure 5 and Supplementary Table 5).

315 **Discussion**

316 As part of a broader study on the ecology of the Asian water monitor lizard and the effect of a

317 changing landscape on its populations in Borneo (Guerrero-Sanchez et al., 2021, 2022), this

318 research investigated one of the consequences of being a generalist carnivore in a human-

319 dominated landscape. There is a wealth of information available on the species in the study area,

320 including its population dynamics and habitat use. Combined with the findings of the current

321 study, this information presents an opportunity to develop a model species that might help us

322 understand the physiological implications of oil palm for animal communities in Borneo.

323 Dietary diversity

324	Environmental changes that drive animal populations to dietary shifts have a substantial impact
325	on animal physiology and can result in cascading effects across interaction networks, including
326	host-parasite interactions (Prange et al., 2003; Ezenwa, 2004; Kaneko and Maruyama, 2005;
327	Liker et al., 2008). In Southeast Asia, large areas of forest have been converted to extensive
328	agriculture, providing Asian water monitor lizards, and other meso-predators, with habitats
329	where foraging efforts are considerably lower than in natural habitats, and where rewards,
330	represented by abundant sources of animal protein and human subsidies, are significantly higher
331	(Becker et al., 2015; Jennings et al., 2015; Guerrero-Sanchez et al., 2022). Our study shows that
332	oil palm plantations provide monitor lizards with a lower dietary diversity than the surrounding
333	forest, resulting in consequences to both their physiology and encounter with novel parasites
334	(Jessop, 2012; Smyth et al., 2014; Wells et al., 2018). Previous research indicated that the
335	relative abundance of rodents in the Kinabatangan floodplain was not different between forest
336	and the surrounding oil palm plantations (Guerrero-Sanchez et al., 2022). Nonetheless, in this
337	study rodents represented the dominant prey group collected from the vomit of plantation lizards,
338	with only a few records from the forest. A study on habitat use of Bornean leopard cats
339	(Prionailurus bengalensis) suggested that the homogeneous structure of oil palm habitats
340	facilitate the capture of rodents, over than in natural forests, where habitat heterogeneity provides
341	shelter and protection for small mammals (Rajaratman et al., 2007). Despite the similar
342	abundances found in both habitats, the higher number of rodents recorded from the stomach

343 content in plantation lizards, compared to those in the forest, is consistent with the344 aforementioned study.

345 Body condition and biochemistry

Our main assumption was based on the hypothesis that monitor lizards inhabiting oil palm
plantations would have a higher body condition index, as well as higher levels of diet-related
biomarkers. However, our results showed the opposite regarding both total and LDL-cholesterol,
which were significantly higher in forested areas. This could be influenced by the low levels of
LDL-cholesterol we found in Kuril estate, which also presents the highest species richness in the
dietary inventory among oil palm sites.

352 The interaction between two different habitats (natural forest and oil palm plantations, in this 353 case) can affect, either positively or negatively, the composition and structure of animal 354 communities, as well as species distribution and behaviour (Potts et al., 2015). For Asian water 355 monitor lizards, variations in prey community structure between edge and interior areas also 356 influence individual movement and population distribution (Jessop et al., 2012). A previous 357 study showed no differences in lizards' abundance and body size between oil palm plantations 358 and forested areas (Guerrero-Sanchez et al., 2021). However, the distribution of abundance and 359 body size in narrow patches of forest showed a tendency towards the mean values observed in 360 plantation sites, suggesting an influence of anthropogenic habitats on adjacent forest, i.e., an 361 edge effect. Here, this edge-effect extends to the physiology of the population, where both body 362 condition and lipid levels of lizards in Lot 5 are similar to lizards inhabiting the adjacent oil palm

363	estate (Hillco). However, the dietary inventory does not present similarities between these two
364	sites. Hence, the edge-effect in this case would not necessarily apply to the distribution of both
365	prey and lizards, but it could be related to the physiology of the prey. An experimental study
366	carried out by Mayntz and Toft (2001), for example, concluded that variations in wolf spiders'
367	metabolites depended on the nutrient composition of the prey's diet. The effect of prey's food on
368	the predator's nutrient intake is worth considering in future studies.
369	From an animal's perspective, physiological biomarkers are a valuable tool to understand
370	environmental changes (Cooke et al., 2013). They are not only highly sensitive to environmental
371	alterations, but their variations are often related to fitness components that drive population
372	persistence (Bergman et al., 2019). Lipids, triglycerides, and cholesterol are important
373	metabolites derived from the metabolism of carbohydrates and lipids (Meyer and Harvey, 2004).
374	As a secondary source of energy, their levels are not only associated with food quality, but also
375	with individuals' activity patterns, where sedentary behavior can lead to an energy demand-
376	intake imbalance. To explore the effects of such behavior on body condition and biochemical
377	levels, we incorporated previous information of home range sizes for the same population
378	(Guerrero-Sanchez et al., 2022), showing that lizards with larger home ranges spend more time
379	roaming between different core areas than those inhabiting oil palm plantations. Our findings
380	suggest that sedentary behavior, coupled with low diverse diets, specially based on small
381	mammals (<i>i.e.</i> , rodents; Kaneko and Maruyama 2005), lead to higher levels of low-density
382	lipoproteins (LDL) cholesterol, known to be associated with cardiovascular disorders (Meyer and
383	Harvey, 2004). On the other hand, high values of high-density lipoproteins (HDL), cholesterol

384	and triglycerides, are associated with a higher dietary diversity in lizards with larger home
385	ranges, and are more likely to be associated with the demand of energy required to constantly
386	roam between core areas. Similarly, to the LDL-cholesterol, these two lipids are associated with
387	energy metabolism, but can be metabolized faster when energy demand exceeds the intake.
388	The effects of habitat type on electrolytes, such as potassium and chloride, could be a
389	consequence of the ingestion of processed food, either directly or through the food web (Jessop
390	et al., 2012). Total proteins, on the other hand, seem to increase with dietary diversity, but the
391	effect is more intense in oil palm habitats. As a carnivorous generalist, the diet of a monitor
392	lizard has a high protein content. However, our findings suggest a stronger correlation in oil
393	palm plantations than in forested areas, which could be explained by the biomass intake rather
394	than by the actual dietary diversity. Additionally, higher levels of globulin in lizards inhabiting
395	oil palm plantations, compared with those living in forest sites, could be an effect likely
396	determined by the higher exposure to pathogens (<i>i.e.</i> , parasitic helminths) in oil palm than in
397	forest sites. Overall, our findings regarding home range size, highlight the importance of
398	improving both size and quality of forest patches within oil palm plantations, such as high
399	conservation value areas, in order to increase prey diversity, and promote larger animal mobility
400	(Guerrero Sanchez et al., 2022). These changes in land-use management would not only benefit
401	the physiological health of the Asian water monitor lizard population, and other generalist
402	species in the area, but it also has been suggested to benefit the survival of other species such as
403	orangutans (Pongo spp.; Ancrenaz et al., 2021).

404 Diet and parasite community

405 Diet is the host trait most strongly associated with the composition of helminth communities 406 (Leung and Koprivnikar, 2019). Soil-transmitted parasites, such as capillarids, trichurids, 407 strongyles, *Strongyloides* and oxyurids have simple and direct life cycles that can be transmitted 408 either from the environment or through predation, while other parasites such as spirurids, 409 cestodes and trematodes have complex life cycles and need one or more intermediate hosts to 410 develop into infecting stages (Galaktionov and Dobrovolskij, 2003). In this study, more diverse 411 diets were associated with a higher prevalence of trichurids and strongyles, which forest lizards 412 might encounter while foraging in the forest. Less diverse diets, on the other hand, were related 413 to a higher prevalence of *Strongyloides*, oxyurids and capillarids, which are parasites prevalent 414 in rodents (Wells et al., 2007; Frias, Pers. Obs.) that could have been transmitted trophically to 415 the lizards.

The higher presence of invertebrates in the stomach of lizards in forested areas, compared with 416 417 those in oil palm plantations, is consistent with the presence of trematodes and cestodes in 418 natural habitats. However, a highly diverse dietary content also influences the low prevalence of 419 such parasites. Although lizards generally inhabit partially inundated habitats, the presence of 420 two large oxbow lakes in Lot 6 can favor the life cycle of digenean trematodes, which have free-421 living aquatic stages, and require specific conditions for successful transmission (Galaktionov 422 and Dobrovolskij, 2003). At the same time, lizards living in aquatic habitats may be more likely 423 to feed on animals that contain trematode infective stages (Combes et al., 1994). We should not

424	discard the presence of a research station in Lot 6, and the intense human activity in the area, and
425	its role in the high parasite prevalence, very similar to those found in oil palm estates.
426	Anthropogenic habitats can alter host-parasite interactions, and lead to either increased or
427	decreased infection risk (Patz et al., 2000; Gillespie and Chapman 2006; Lafferty et al., 2006;
428	Cardoso et al., 2016; Bonell et al., 2018). Lizards having diverse parasite communities maintain
429	a healthy balance among parasite populations (Lafferty et al., 2006). But when such balance is
430	disturbed, it leads to the increase of certain parasite groups, and negatively impact the individual
431	fitness and the population survival (Frias and MacIntosh, 2019). By decreasing their foraging
432	activities in the forest, plantation lizards also decrease their encounters with parasites with
433	complex life cycles. Similarly, having rodents as a predictable food source can increase the
434	prevalence of helminths transmitted through prey ingestion in plantation lizards (Lafferty et al.,
435	2006; Dunne et al., 2013; Leung and Koprivnikar, 2019). We also observed a significant
436	association between body condition and both parasite richness and intensity of infection in
437	plantation lizards, where smaller lizards hosted fewer parasite species, and shed more parasite
438	infective stages into the environment. This observation suggests that homogeneous diets may
439	alter host parasite communities, and potentially impact individual fitness (Lafferty et al., 2006;
440	Frias and MacIntosh, 2019).

441 The *fast-food effect*: the role of dietary diversity and sedentarism on

442 population health

443 Fast-food, as we know it, is usually associated with hyper-caloric meals that are quick, 444 convenient, and low-priced. Long-term consumption of fast-food is also associated with obesity 445 and cardiovascular disorders (Rosenheck, 2001; Alter and Eny, 2005), and the proximity of fast-446 food restaurants to schools has been linked to obesity in teenagers in the USA (Davis and 447 Carpenter, 2009). Similarly, human-dominated landscapes, especially industrial crops, and 448 farms, offer neighboring wildlife abundant food resources that are easily accessible, convenient, 449 and have similar health consequences to animal populations (Murray et al., 2015), hence a fast-450 food effect. Although the impact of the fast-food effect may not be immediately noticeable for 451 lizards and other reptiles, it could pose a risk for mammals and birds that have adapted to similar 452 landscapes and are more sensitive to physiological changes (Becker et al., 2015; Murray et al., 453 2015; Murray et al., 2016). The Asian water monitor lizard is a widespread, highly adaptable, 454 and long-lived species, commonly found in human-altered landscapes. These life history traits 455 make it a fitting model species to help us understand the physiological threats posed by changing 456 ecosystems.

457 Fast-food consumption in humans is a complex health issue that not only involves obesity and 458 cardiovascular disorders, but implies a cascade of social, economic, and cultural causes and 459 consequences (Rosenheck, 2001; Davis and Carpenter, 2009). Likewise, the fast-food effect in 460 wildlife involves a complex series of elements that need to be understood by observing different 461 aspects of wildlife ecology (*i.e.*, prey abundance and distribution, human subsides, demography, 462 distribution, activity patterns of target species, *etc.*), and not only by comparing populations in 463 different habitats. Aside from dietary diversity and movement ranges, other important elements 464 to consider are biomass intake, including the nutritional properties of prey, and parasites present

465	in prey communities. While the first element would offer a more complete picture of how energy
466	intake is used and metabolized by predators, a wider knowledge of parasite communities
467	infecting prey would help us understand transmission pathways through food webs (Lafferty et
468	al., 2006). Additional demographic and longitudinal information would be important
469	complements to evaluate the impact of the <i>fast-food effect</i> on individual fitness.
470	The metabolic responses of lizards and the changes in parasite community composition,
471	influenced by a diet derived from landscape alterations, suggests a decreased physiological status
472	and fitness in the wildlife community in the area. The abundance and high catchability rate of
473	Asian water monitor lizards (Guerrero-Sanchez et al., 2021) allowed us to generate more data
474	than it would have been possible by targeting other wildlife species living in similar habitats,
475	which are more cryptic or have a lower catchability rate, such as leopard cats (Prionailurus
476	bengalensis, civets (Viverra tangalunga and Paradoxurus hermaphroditus), macaques (Macaca
477	fascicularis and M. nemestrina), and bearded pigs (Sus barbatus), among others. Such
478	information provides a hint towards the hidden consequences that living in disturbed ecosystems
479	can have for other species as well.
480	Finally, this study presents the most robust data on blood biochemistry for the Asian water

481 monitor lizard in the wild. Although none of the sampled individuals showed signs of being

482 unhealthy, it remains to be explored whether these metabolite levels lay or not within healthy

- 483 ranges for populations living in the forest and in plantations. To our knowledge, there is no
- 484 reference database that allows for an accurate comparison of our results. The International
- 485 Species Information System (https://www.species360.org/) is the most comprehensive biometric

- 486 database for animal information, however, it is mostly composed of samples from captive
- 487 animals with different dietary schemes. Hence, we recommend caution when using the
- 488 information presented here as reference for the species.

489 Supplementary Material

490 Supplementary material is available online.

491 **Data Availability**

492 The data underlying this article will be shared on reasonable request to the first author (SGS).

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506 Ethics and Animal Welfare Statement

Animal trapping, handling, and sampling protocols were designed and conducted by a certified
veterinarian (SGS), in accordance with animal welfare guidelines from the National Centre for
Replacement, Refinement and Reduction of Animals in Research (NC3RS). Protocols were
submitted, reviewed, and authorized by Sabah Wildlife Department and Sabah Biodiversity
Centre, as part of the procedures to authorize access to natural resources (access license
JKM/MBS.1000-2/2 JLD.3-7).

513 Author contributions

Guerrero-Sanchez*: Conceptualization, methodology, statistical analysis, investigation, writing
and editing original draft; Frias*: Methodology, parasitological analysis, statistical analysis,
investigation, writing and editing original draft; Orozco-terWengel: Supervision and editing
original draft; Saimin: Resources and editing original draft; Goossens: Supervision, project
administration, and editing original draft.

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520 Conflict of Interest

521 The authors declare no conflict of interest.

to Review Only

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Figure 1. Study area in Malaysian Borneo (top left corner). Trapping sites (red frame) were distributed across three forest lots and three oil palm estates within the Lower Kinabatangan

Wildlife Sanctuary (yellow frame). Images are representative of both forest (bottom left) and oil palm plantation (top right) sites. The lizard in the top centre is one of the sampled individuals weighting ~20 Kg.

Figure 2. Diet inventory identified in the vomit of Asian water monitor lizards.

Figure 3. Graphic representation of the impact of dietary diversity on the biochemical markers of Asian water monitor lizards. Forest lizards have a more diverse prey availability, while those living in oil palm plantations primarily feed on rodents (a). The impact of dietary diversity on certain biochemical markers varies in magnitude and direction based on the type of habitat (b). Additionally, the effect of dietary diversity on body condition and lipids is enhanced by the size of an individual's home range, with smaller ranges intensifying the negative correlation between dietary diversity and these biomarkers (c).

Figure 4. Predictive effects of dietary diversity on body condition, low and high density lipoprotein cholesterol, triglycerides, and its variation based on lizards' home range sizes. Home range, estimated as Local Convex Hull with adaptive algorithm, is expressed in km².

Figure 5. Graphic representation of the impact of dietary diversity on parasite communities associated to the Asian water monitor lizard. Oil palm plantations are associated to a decrease in parasite species richness and a higher parasite prevalence (a). In contrast, in forested areas, an increase in dietary diversity leads to an increase in both the number of parasite taxonomic groups (richness) and parasite prevalence (b).

Duors true o		Forest		Oil p	alm plan	plantation	
r rey type –	Lot 5	Lot 6	Lot 7	Hillco	Корі	Kuril	
Arthropods							
Centipede	4	1	3	2	1	3	
Crab	10	6	5	0	0	0	
Scorpion	1	0	1	0	0	0	
Woodlouse	4	3	10	2	2	8	
Amphibians							
Frog	5	1	2	0	1	0	

Table 1. Dietary diversity, presented as Shannon-Wiener Index (H'), calculated for	prey items
identified in the vomit of Asian water monitor lizards.	

Fish						
Catfish	0	4	1	0	2	5
Reptiles						
Egg (snake)	1	1	0	0	0	0
Snake	1	1	0	0	1	0
Tortoise	1	1	1	0	1	0
Mollusca						
Snail	3	3	4	0	2	1
Mammals						
Bat	0	1	0	0	0	0
Macaque	1	0	1	0	0	0
Rodent	3	2	2	24	20	18
Wild boar	1	0	0	0	0	0
H′	2.162	2.167	1.978	0.509	1.265	1.269

Table 2. Significant outcomes of the statistical analysis carried out for the biochemical markers and parasite prevalence and richness. Here we only presented the significant results. The full outcome is presented in the supplementary material.

O Pere

Statistic	Dependent variable	Independent variable	Outcome
		BIOCHEMICAL MARKERS	
	Total cholesterol	Forest v. oil palm	$Xt^2 = 2.80, p = 0.03$
	Total proteins	Forest v. oil palm	$Xi^2 = 446.66, p = 0.01$
	Globulin	Forest v. oil palm	$Xi^2 = 0.10, p = 0.02$
	Total cholesterol	All sites	$Xi^2 = 18.36, p = 0.03$
	LDL-cholesterol	All sites	$Xi^2 = 9.16, p < 0.01$
	HDL-cholesterol	All sites	$Xi^2 = 2.61, p < 0.01$
GLM*	Total proteins	All sites	<i>Xi</i> ² = 898.17, p = 0.03
	Albumin	All sites	$Xi^2 = 136.53, p = 0.05$
	HDL-cholesterol	Forest sites	$Xi^2 = 2.01, p = 0.01$
	Total cholesterol	Oil palm sites	<i>Xi</i> ² = 14.20, p < 0.01
	LDL-cholesterol	Oil palm sites	$Xi^2 = 7.18, p < 0.01$
	Total proteins	Oil palm sites	<i>Xt</i> ² = 390.84, p = 0.04
	Albumin	Oil palm sites	<i>Xt</i> ² = 113.59, p = 0.01

	LDL-cholesterol	Dietary diversity (F [†])	$\beta = -0.37 \ (0.16), \ p = 0.038$
	LDL-cholesterol	Dietary diversity (OPP ^{††})	$\beta = -0.80 \ (0.33), p = 0.016$
	HDL-Cholesterol	Dietary diversity (F [†])	$\beta = -0.12 (0.05), p = 0.022$
	HDL-Cholesterol	Dietary diversity (OPP ^{††})	$\beta = -0.20 \ (0.08), \ p = 0.009$
	Triglycerides	Dietary diversity (F [†])	$\beta = 0.07 \ (0.28), p = 0.81$
	Triglycerides	Dietary diversity (OPP ^{††})	$\beta = -1.46 (0.47), p = 0.002$
CEE44	Total protein	Dietary diversity (F [†])	$\beta = 5.33 (2.32), p = 0.021$
GEE**	Total protein	Dietary diversity (OPP ^{††})	<i>β</i> = 21.60 (5.82), p < 0.001
	Potassium	Dietary diversity (F [†])	$\beta = -2.23 (0.19), p = 0.061$
	Potassium	Dietary diversity (OPP ^{††})	$\beta = -5.25 (1.98), p = 0.008$
	Body condition	Dietary diversity + HR ^ç	$\beta = 0.33 (0.11), p = 0.003$
	LDL-cholesterol	Dietary diversity + HR ^ç	<i>B</i> = 1.24 (0.33), p < 0.001
	HDL-cholesterol	Dietary diversity + HR ^ç	$\beta = 0.24 \ (0.12), p = 0.043$
	Tryglicerides	Dietary diversity + HR ^ç	$\beta = 1.13 \ (0.68), p = 0.002$
		PARASITES	
	Prevalence	Forest v oil nalm	V2 125 ((
	110,000	r orest v: on pann	$X^2 = 125.00, p < 0.001$
	Prevalence	All sites	$X^{2} = 125.66, p < 0.001$ $X^{2} = 87258.21, p < 0.001$
CI M*	Prevalence Trichuris prev.	All sites Forest v. oil palm	$X^{2} = 125.66, p < 0.001$ $X^{2} = 87258.21, p < 0.001$ $X^{2} = 2075.20, p < 0.001$
GLM*	Prevalence <i>Trichuris</i> prev. Spirurids	All sites Forest v. oil palm Forest v. oil palm	$X^{2} = 125.66, p < 0.001$ $X^{2} = 87258.21, p < 0.001$ $X^{2} = 2075.20, p < 0.001$ $X^{2} = 864.32, p < 0.001$
GLM*	Prevalence Trichuris prev. Spirurids Oxyurids	All sites Forest v. oil palm Forest v. oil palm Forest v. oil palm	$X^{2} = 125.66, p < 0.001$ $X^{2} = 87258.21, p < 0.001$ $X^{2} = 2075.20, p < 0.001$ $X^{2} = 864.32, p < 0.001$ $X^{2} = 3771.04, p = 0.002$
GLM*	Prevalence Trichuris prev. Spirurids Oxyurids Strongyloides	All sites Forest v. oil palm Forest v. oil palm Forest v. oil palm Forest v. oil palm	$X^{2} = 125.66, p < 0.001$ $X^{2} = 87258.21, p < 0.001$ $X^{2} = 2075.20, p < 0.001$ $X^{2} = 864.32, p < 0.001$ $X^{2} = 3771.04, p = 0.002$ $X^{2} = 1605.39, p < 0.001$
GLM*	Prevalence Trichuris prev. Spirurids Oxyurids Strongyloides Parasite richness	All sites Forest v. oil palm Forest v. oil palm Forest v. oil palm Forest v. oil palm Body condition (F [†])	$X^{2} = 125.66, p < 0.001$ $X^{2} = 87258.21, p < 0.001$ $X^{2} = 2075.20, p < 0.001$ $X^{2} = 864.32, p < 0.001$ $X^{2} = 3771.04, p = 0.002$ $X^{2} = 1605.39, p < 0.001$ $\beta = -0.45 (1.521), p = 0.77$
GLM*	Prevalence Trichuris prev. Spirurids Oxyurids Strongyloides Parasite richness Parasite richness	All sites Forest v. oil palm Forest v. oil palm Forest v. oil palm Forest v. oil palm Body condition (F [†]) Body condition (OPP ^{††})	$X^{2} = 125.66, p < 0.001$ $X^{2} = 87258.21, p < 0.001$ $X^{2} = 2075.20, p < 0.001$ $X^{2} = 864.32, p < 0.001$ $X^{2} = 3771.04, p = 0.002$ $X^{2} = 1605.39, p < 0.001$ $\beta = -0.45 (1.521), p = 0.77$ $\beta = 2.23 (0.739), p = 0.002$
GLM*	Prevalence Trichuris prev. Spirurids Oxyurids Strongyloides Parasite richness Parasite richness Trichuris prevalence	All sites Forest v. oil palm Forest v. oil palm Forest v. oil palm Forest v. oil palm Body condition (F [†]) Body condition (OPP ^{††}) Dietary diversity	$X^{2} = 125.66, p < 0.001$ $X^{2} = 87258.21, p < 0.001$ $X^{2} = 2075.20, p < 0.001$ $X^{2} = 864.32, p < 0.001$ $X^{2} = 3771.04, p = 0.002$ $X^{2} = 1605.39, p < 0.001$ $\beta = -0.45 (1.521), p = 0.77$ $\beta = 2.23 (0.739), p = 0.002$ $\beta = 0.59 (0.27), p = 0.03$
GLM*	Prevalence Trichuris prev. Spirurids Oxyurids Strongyloides Parasite richness Parasite richness Trichuris prevalence Physaloptera prevalence	All sites Forest v. oil palm Forest v. oil palm Forest v. oil palm Forest v. oil palm Body condition (F [†]) Body condition (OPP ^{††}) Dietary diversity Dietary diversity	$X^{2} = 125.66, p < 0.001$ $X^{2} = 87258.21, p < 0.001$ $X^{2} = 2075.20, p < 0.001$ $X^{2} = 864.32, p < 0.001$ $X^{2} = 3771.04, p = 0.002$ $X^{2} = 1605.39, p < 0.001$ $\beta = -0.45 (1.521), p = 0.77$ $\beta = 2.23 (0.739), p = 0.002$ $\beta = 0.59 (0.27), p = 0.03$ $\beta = -0.665 \pm 0.25, p = 0.008$
GLM*	Prevalence Trichuris prev. Spirurids Oxyurids Strongyloides Parasite richness Parasite richness Trichuris prevalence Physaloptera prevalence Strongyloides prevalence	All sites Forest v. oil palm Forest v. oil palm Forest v. oil palm Forest v. oil palm Body condition (F [†]) Body condition (OPP ^{††}) Dietary diversity Dietary diversity Dietary diversity	$X^{2} = 125.66, p < 0.001$ $X^{2} = 87258.21, p < 0.001$ $X^{2} = 2075.20, p < 0.001$ $X^{2} = 864.32, p < 0.001$ $X^{2} = 3771.04, p = 0.002$ $X^{2} = 1605.39, p < 0.001$ $B = -0.45 (1.521), p = 0.77$ $B = 2.23 (0.739), p = 0.002$ $B = 0.59 (0.27), p = 0.003$ $B = -0.665 \pm 0.25, p = 0.008$ $B = -0.374 \pm 0.19, p = 0.058$
GLM* GEE**	Prevalence Trichuris prev. Spirurids Oxyurids Strongyloides Parasite richness Parasite richness Trichuris prevalence Physaloptera prevalence Strongyloides prevalence Parasite richness	All sites Forest v. oil palm Forest v. oil palm Forest v. oil palm Forest v. oil palm Body condition (F [†]) Body condition (OPP ^{††}) Dietary diversity Dietary diversity Dietary diversity Dietary diversity Dietary diversity	$X^{2} = 125.66, p < 0.001$ $X^{2} = 87258.21, p < 0.001$ $X^{2} = 2075.20, p < 0.001$ $X^{2} = 864.32, p < 0.001$ $X^{2} = 3771.04, p = 0.002$ $X^{2} = 1605.39, p < 0.001$ $B = -0.45 (1.521), p = 0.77$ $B = 2.23 (0.739), p = 0.002$ $B = 0.59 (0.27), p = 0.003$ $B = -0.665 \pm 0.25, p = 0.008$ $B = -0.374 \pm 0.19, p = 0.058$ $B = 9.37 (1.62), p < 0.001$
GLM* GEE**	PrevalenceTrichuris prev.SpiruridsOxyuridsStrongyloidesParasite richnessParasite richnessTrichuris prevalencePhysaloptera prevalenceStrongyloidesParasite richnessParasite richnessPhysaloptera prevalenceParasite richnessParasite richnessParasite richnessParasite richnessParasite richnessParasite richness	All sites Forest v. oil palm Forest v. oil palm Forest v. oil palm Forest v. oil palm Body condition (F [†]) Body condition (OPP ^{††}) Dietary diversity Dietary diversity Dietary diversity (F [†]) Dietary diversity (OPP ^{††})	$X^{2} = 125.66, p < 0.001$ $X^{2} = 87258.21, p < 0.001$ $X^{2} = 2075.20, p < 0.001$ $X^{2} = 864.32, p < 0.001$ $X^{2} = 3771.04, p = 0.002$ $X^{2} = 1605.39, p < 0.001$ $\beta = -0.45 (1.521), p = 0.77$ $\beta = 2.23 (0.739), p = 0.002$ $\beta = 0.59 (0.27), p = 0.003$ $\beta = -0.665 \pm 0.25, p = 0.008$ $\beta = -0.374 \pm 0.19, p = 0.058$ $\beta = 9.37 (1.62), p < 0.001$ $\beta = -22.50 (0.36), p < 0.001$
GLM* GEE**	PrevalenceTrichuris prev.SpiruridsOxyuridsStrongyloidesParasite richnessParasite richnessTrichuris prevalencePhysaloptera prevalenceStrongyloidesParasite richnessParasite richnessPhysaloptera prevalenceParasite richnessParasite richnessParasite richnessParasite richnessParasite richnessParasite prevalence	All sites Forest v. oil palm Body condition (F [†]) Body condition (OPP ^{††}) Dietary diversity Dietary diversity Dietary diversity (F [†]) Dietary diversity (OPP ^{††}) Dietary diversity (F [†])	$X^{2} = 125.66, p < 0.001$ $X^{2} = 87258.21, p < 0.001$ $X^{2} = 2075.20, p < 0.001$ $X^{2} = 2075.20, p < 0.001$ $X^{2} = 864.32, p < 0.001$ $X^{2} = 3771.04, p = 0.002$ $X^{2} = 1605.39, p < 0.001$ $\beta = -0.45 (1.521), p = 0.77$ $\beta = 2.23 (0.739), p = 0.002$ $\beta = 0.59 (0.27), p = 0.003$ $\beta = -0.665 \pm 0.25, p = 0.008$ $\beta = -0.374 \pm 0.19, p = 0.058$ $\beta = 9.37 (1.62), p < 0.001$ $\beta = -22.50 (0.36), p < 0.001$ $\beta = 32.8 (12.1), p = 0.007$

*Generalised linear model; **Generalised Estimation Equations; [†]Forest; ^{††}Oil palm plantation; ^eHome range size

Table 3. Parasites reported from lizards' faeces. Values show prevalence (%) by site, followed by the number of positive individuals for each parasite. Overall prevalence per site and habitat type, as well as parasite richness, are included in the lower rows of the table.

, u e n e	n no pui no		, 		10	0 01 0110 00	
Parasite	Lot 5	Lot 6	Lot 7	Forest	Hillco	Kopi	Oil palm
taxonomic group	(n=12)	(n=5)	(n=14)	(n=31)	(n=12)	(n=30)	(n=41)

Nematodes							
Ascaris spp.	0	0	7.1 (1)	3.1 (1)	0	0	0
<i>Capillaria</i> spp.	53.9 (7)	0	35.7 (5)	37.5 (12)	41.7 (5)	48.3 (14)	46.3 (19)
Oxyurida spp.	53.9 (7)	0	50 (7)	43.8 (14)	58.3 (7)	17.2 (5)	29.3 (12)
Physaloptera spp.	7.7 (1)	20 (1)	0	6.2 (2)	16.7 (2)	0	4.9 (2)
Spirurida spp.	7.7 (1)	20 (1)	7.1 (1)	9.4 (3)	8.3 (1)	0	2.4 (1)
Strongylida spp.	15.4 (2)	80 (4)	7.1 (1)	21.9 (7)	16.7 (2)	34.5 (10)	29.3 (12)
Strongyloides spp.	30.8 (4)	0	0	12.5 (4)	25 (3)	20.7 (6)	22 (9)
Trichuris spp.	7.7 (1)	40 (2)	14.3 (2)	15.6 (5)	0	6.9 (2)	4.9 (2)
Cestodes							
Cestoda	0	0	7.1 (1)	12.5 (1)	8.3 (1)	0	2.4 (1)
Trematodes							
Trematoda	0	60 (3)	0	9.4 (3)	0	0	0
Overall prevalence	76.9 (10)	80 (4)	71.4 (10)	74.9 (24)	83.3 (10)	80 (24)	80.9 (34)
Parasite species richness	7	5	7	10	7	5	8



Figure 1. Study area in Malaysian Borneo (top left corner). Trapping sites (red frame) were distributed across three forest lots and three oil palm estates within the Lower Kinabatangan Wildlife Sanctuary (yellow frame). Images are representative of both forest (bottom left) and oil palm plantation (top right) sites. The lizard in the top centre is one of the sampled individuals weighting ~20 Kg.

184x134mm (300 x 300 DPI)



Figure 2. Diet inventory identified in the vomit of Asian water monitor lizards.

190x127mm (300 x 300 DPI)



Figure 3. Graphic representation of the impact of dietary diversity on the biochemical markers of Asian water monitor lizards. Forest lizards have a more diverse prey availability, while those living in oil palm plantations primarily feed on rodents (a). The impact of dietary diversity on certain biochemical markers varies in magnitude and direction based on the type of habitat (b). Additionally, the effect of dietary diversity on body condition and lipids is enhanced by the size of an individual's home range, with smaller ranges intensifying the negative correlation between dietary diversity and these biomarkers (c).

186x144mm (300 x 300 DPI)



Figure 4. Predictive effects of dietary diversity on body condition, low and high density lipo-protein cholesterol, triglycerides, and its variation based on lizards' home range sizes. Home range, estimated as Local Convex Hull with adaptive algorithm, is expressed in km².

188x139mm (300 x 300 DPI)



Figure 5. Graphic representation of the impact of dietary diversity on parasite communities associated to the Asian water monitor lizard. Oil palm plantations are associated to a decrease in parasite species richness and a higher parasite prevalence (a). In contrast, in forested areas, an increase in dietary diversity leads to an increase in both the number of parasite taxonomic groups (richness) and parasite prevalence (b).

187x131mm (300 x 300 DPI)

Supplementary material

Supplementary Table 1. Mean value of body measurements and biochemical parameters analyzed for Asian water monitor lizards.

Parameter	Lot 5	Lot 6	Lot 7	Forest	Hillco	Kopi	Kuril	Plantation
Body measurem	ents							
Weight	5.98±3.77	5.76±4.98	5.27±4.49	5.67±4.5	6.15±3.33	6.05±3.63	6.02±3.65	6.07±3.52
(Kg.)	(1.5-16.5)	(1.5-22)	(1-18)	(1-22)	(1.5-11.6)	(2-15)	(2-17)	(1.5-17)
	n=24	n=40	n=28	n=92	n=28	n=53	n=25	n=106
Body	0.39±0.14	0.34±0.17	0.35±0.13	0.35±0.15	0.39±0.12	0.39±0.13	0.39±0.12	0.39±0.12
condition	(0.11-0.65)	(0.03-0.67)	(0.17-0.63)	(0.03-0.67)	(0.11-0.57)	(0.17-0.60)	(0.18-0.63)	(0.11-0.63)
	n=24	n=40	n=28	n=92	n=28	n=53	n=25	n=106
Lipids								
Cholesterol	2.21±0.67	2.04±0.63	1.89±0.70	2.04±0.67	2.17±0.84	1.43±0.82	2.17±0.54	1.8±0.85
(mmol/L)	(1.20-3.60)	(1.20-4.70)	(0.80-3)	(0.80-4.70)	(0.80-4.20)	(0.07-5.0)	(1.30-3.70)	(0.07-5.0)
	n=24	n=40	n=28	n=92	n=28	n=52	n=24	n=104
LDL-Ch	1.68±0.85	1.59±0.62	1.79±2.14	1.68±1.34	1.76±0.82	0.97±0.66	1.73±0.71	1.36±0.81
(mmol/L)	(0.1-3.25)	(0.22-2.62)	(0.66-11.6)	(0.1-11.6)	(0.29-3.44)	(0.1-2.72)	(0.25-3.53)	(0.1-3.53)
	n=21	n=31	n=25	n=77	n=24	n=42	n=19	n=85
HDL-Ch	0.18±0.14	0.11±0.03	0.19±0.20	0.15±0.14	0.13±0.07	0.14±0.06	0.11±0.04	0.13±0.06
(mmol/L)	(0.1-0.59)	(0.1-0.22)	(0.1-0.82)	(0.1-0.82)	(0.1-0.4)	(0.1-0.4)	(0.1-0.29)	(0.1-0.4)
	n=22	n=32	n=27	n=81	n=25	n=47	n=24	n=96
Triglycerides	1.62 ± 2.58	2.18±3.57	2.47 ± 4.54	2.12±3.67	1.33 ± 2.03	0.98±1.73	1.97±2.59	1.31±2.06
(mmol/L)	(0.05-9.92)	(0.1-15.26)	(0.05-20.87)	(0.05-20.87)	(0.05-9.13)	(0.05-8.99)	(0.06-10.28)	(0.05-10.28)
	n=23	n=34	n=28	n=85	n=25	n=49	n=24	n=98

Values presented as mean \pm SD; (min - max), and sampling size (n).

values presented as mean $\pm 5D$, (nim - max), and sampling size (n).								
Parameter	Lot 5	Lot 6	Lot 7	Forest	Hillco	Корі	Kuril	Plantation
Proteins								
Total protein	78.1±8.33	76.6±9.44	75.1±7.23	76.6±8.71	77.6±10.8	83.6±6	79.5±6.49	80.3±8.18
(g/L)	(62-88)	(56-96)	(63-83)	(56-96)	(56-106)	(69-94)	(65-90)	(56-106)
	n=13	n=39	n=15	n=67	n=20	n=21	n=24	n=65
Albumin	26.1±2.9	25.5±4.03	25.3±2.25	25.6±3.47	24.4±5.4	27.6±1.86	26.8±2.56	26.3±3.72
(g/L)	(20-30)	(10-34)	(21-28)	(10-34)	(10-30)	(23-31)	(22-34)	(10-34)
	n=13	n=39	n=15	n=67	n=20	n=21	n=24	n=65
Globulin	52±5.76	51.3±7.28	49.9±5.76	51.1±6.64	53.8±13.2	56±4.32	52.8±4.94	54.1±8.24
(g/L)	(42-60)	(36-66)	(39-57)	(36-66)	(36-100)	(46-65)	(43-60)	(36-100)
	n=13	n=39	n=15	n=67	n=20	n=21	n=24	n=65
Uric acid	0.67±0.31	0.65±0.29	0.66±0.45	0.66±0.35	0.60±0.22	0.5±0.31	0.65±0.30	0.56±0.29
(mmol/L)	(0.27-1.44)	(0.17-1.49)	(0.1-2.42)	(0.1-2.42)	(0.22-1.07)	(0.13-1.33)	(0.17-1.53)	(0.13-1.53)
	n=24	n=40	n=28	n=92	n=28	n=52	n=24	n=104
Electrolytes								
Sodium	157±4.84	160±5.49	157±4.33	159±5.28	160±5.65	161±4.31	161±7.07	161±5.84
(mmol/L)	(146-164)	(152-172)	(152-167)	(146-172)	(145-167)	(152-170)	(136-171)	(136-171)
	n=13	n=39	n=15	n=67	n=20	n=21	n=25	n=66
Potassium	31.8±8.16	30.6±5.48	31.8±6.56	31.1±6.28	33.3±7.9	30.7±3.7	29.9±7.49	31.2±6.71
(mmol/L)	(24.4-56.1)	(20.4-43)	(25.7-50.4)	(20.4-56.1)	(24.7-58)	(24.4-37.2)	(22.7-50.7)	(22.7-58)
	n=13	n=34	n=12	n=59	n=19	n=21	n=25	n=65
Chloride	99.3±6.56	102±6.03	103±4.51	102±5.9	105±6.21	103 ± 5.48	103±5.75	104±5.83
(mmol/L)	(80-109)	(85-112)	(96-111)	(80-112)	(91-116)	(87-110)	(89-111)	(87-116)
	N=13	n=39	n=15	n=67	n=20	n=21	n=25	n=66

Supplementary Table 1 (cont.). Mean value of body measurements and biochemical parameters analyzed for Asian water monitor lizards. Values presented as mean \pm SD: (min - max), and sampling size (n).

Marker	Variable	Xi^2	р
	Habitat	0.06	0.06
Body condition	Sites	0.11	0.31
Douy condition	Forest sites	0.05	0.35
	Oil palm plantation sites	0.00	0.96
	Habitat	2.80	0.03
Total cholesterol	Sites	18.30	< 0.001
	Forest sites	1.35	0.21
	Ull palm plantation sites	14.20	< 0.001
	Habitat	1.//	U.U0
LDL - cholesterol	Sites	9.16	< 0.001
	Forest sites	0.20	0.84
	Oil palm plantation sites	7.18	< 0.001
	Habitat	0.14	0.38
HDL - cholesterol	Sites	2.61	0.01
	Forest sites	2.01	0.02
	Oil palm plantation sites	0.47	0.13
	Habitat	3.33	0.25
Triclycoridos	Sites	16.49	0.26
Ingrycenues	Forest sites	1.95	0.71
	Oil palm plantation sites	11.21	0.08
	Habitat	446.66	0.01
T (1 (1	Sites	898.17	0.03
lotal proteins	Forest sites	60.67	0.68
	Oil palm plantation sites	390.84	0.04
	Habitat	18.09	0.24
	Sites	136.53	0.05
Albumin	Forest sites	4.85	0.82
	Oil palm plantation sites	113.59	0.01
	Habitat	0.10	0.02
	Sites	0.17	0.10
Globulin	Forest sites	0.01	0.70
	Oil palm plantation sites	0.05	0.25

Supplementary Table 2. Differences in body condition and biochemical markers among habitat type, sites, and sites grouped per habitat type.

Marker	Variable	Xi ²	р
	Habitat	1.15	0.04
Uric acid	Sites	2.57	0.11
one actu	Forest sites	0.03	0.96
	Oil palm plantation sites	1.39	0.08
	Habitat	81.14	0.11
Sodium	Sites	274.49	0.11
Sourum	Forest sites	153.03	0.06
	Oil palm plantation sites	40.32	0.56
	Habitat	0.00	0.96
D / · ·	Sites	0.15	0.50
Potassium	Forest sites	0.02	0.77
	Oil palm plantation sites	0.14	0.15
	Habitat	104.14	0.08
	Sites	303.33	0.11
Chloride	Forest sites	113.72	0.19
	Oil palm plantation sites	85.47	0.28

Supplementary Table 2 (cont.) Differences in body condition and biochemical markers among habitat type, sites, and sites grouped per habitat type.

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Supplementary Table 3. Generalized estimation equations (GEE) models outcomes for the effect of body condition and dietary diversity, as estimated with the Shannon-Wiener Index (H'), on the biochemical markers of Asian water monitor lizards based on habitat type.

on naonat type.								
Body condition	ß	Std. Err.	W	р				
(Intercept)	2.531	0.2690	88.45	<2e-16				
Dietary diversity : forest	0.1408	0.1507	0.87	0.35				
Dietary diversity : OPP	0.0364	0.2558	0.02	0.89				
Total cholesterol	ß	Std. Err.	W	р				
(Intercept)	2.545	0.301	71.28	<2e-16				
Dietary diversity : forest	-0.224	0.155	2.10	0.15				
Dietary diversity : OPP	-0.555	0.347	2.56	0.11				
LDL – cholesterol	ß	Std. Err.	W	р				
(Intercept)	2.226	0.332	44.86	2.1e-11				
Dietary diversity : forest	-0.336	0.162	4.30	0.038				
Dietary diversity : OPP	-0.801	0.332	5.84	0.016				
HDL - cholesterol	ß	Std. Err.	W	р				
(Intercept)	0.3884	0.0967	16.13	5.9e-05				
Dietary diversity : forest	-0.1187	0.0518	5.25	0.022				
Dietary diversity : OPP	-0.2020	0.0776	6.78	0.009				
Triglycerides	ß	Std. Err.	W	р				
(Intercept)	2.4601	0.4725	27.10	1.9e-07				
Dietary diversity : forest	0.0671	0.2789	0.06	0.809				
Dietary diversity : OPP	-1.4583	0.4665	9.77	0.0018				
Total protein	ß	Std. Err.	W	р				
(Intercept)	63.23	4.42	204.41	< 2e-16				
Dietary diversity : forest	5.33	2.32	5.29	0.02144				
Dietary diversity : OPP	21.55	5.82	13.73	0.00021				
Albumin	ß	Std. Err.	W	р				
(Intercept)	22.56	2.53	79.56	<2e-16				
Dietary diversity : forest	1.43	1.20	1.41	0.234				
Dietary diversity : OPP	3.64	2.05	3.14	0.077				
Globulin	ß	Std. Err.	W	р				
(Intercept)	52.809	3.164	278.62	<2e-16				
Dietary diversity : forest	-0.729	1.593	0.21	0.65				
Dietary diversity : OPP	1.231	2.748	0.20	0.65				

Supplementary Table 3 (cont.). Generalized estimation equations (GEE) models outcomes for the effect of body condition and dietary diversity, as estimated with the Shannon-Wiener Index (H'), on the biochemical markers of Asian water monitor lizards based on habitat type.

Uric acid	ß	Std Err	W	n
(Intercept)	0.6352	0 1071	35 19	е-09
Dietary diversity : forest	0.0163	0.0537	0.09	0.76
Dietary diversity · OPP	-0.0429	0.1201	0.13	0.72
Sodium	ß	Std. Err.	W	р р
(Intercept)	163.13	2.37	4722.59	<2e-16
Dietary diversity : forest	-1.23	1.14	1.17	0.28
Dietary diversity : OPP	-2.79	1.98	1.99	0.16
Potassium	ß	Std. Err.	W	р
(Intercept)	35.85	2.50	205.03	<2e-16
Dietary diversity : forest	-2.23	1.19	3.50	0.0613
Dietary diversity : OPP	-5.25	1.98	6.99	0.0082
Chloride	ß	Std. Err.	W	Р
(Intercept)	102.58	4.09	630.23	<2e-16
Dietary diversity : forest	-2.83	2.02	1.96	0.16
Dietary diversity : OPP	-5.19	3.95	1.73	0.19

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Supplementary Table 4. Generalized estimation equations (GEE) models outcomes for the effect of body condition and dietary diversity, as estimated with the Shannon-Wiener Index (H'), on the biochemical markers of Asian water monitor lizards based on home range size. Home range (HR) was estimated using Local Convex Hull and

	expressed	I III KIII .		
Body condition	ß	Std. Err.	W	р
(Intercept)	0.4917	0.0423	135.29	<2e-16
Dietary diversity (H')	0.0596	0.0294	4.11	0.0427
Home range	0.2648	0.0677	15.29	9.2e-05
Dietary diversity * HR	-0.1221	0.0454	7.22	0.0072
Total cholesterol	ß	Std. Err.	W	Р
(Intercept)	3.839	1.609	5.69	0.017
Dietary Diversity (H')	-1.411	0.797	3.14	0.077
Home range	-3.091	2.999	1.06	0.303
Dietary diversity * HR	1.712	1.408	1.48	0.224
LDL - cholesterol	ß	Std. Err.	W	р
(Intercept)	-1.158	0.427	7.37	0.0066
Dietary Diversity (H')	1.566	0.318	24.27	8.4e-07
Home range	0.843	0.434	3.77	0.0521
Dietary diversity * HR	-0.992	0.280	12.54	0.0004
HDL - cholesterol	ß	Std. Err.	W	р
(Intercept)	-0.493	0.642	0.59	0.4421
Dietary Diversity (H')	-0.782	0.260	9.07	0.0026
Home range	-3.234	1.479	4.78	0.0287
Dietary diversity * HR	1.425	0.649	5.00	0.0254
Triglycerides	ß	Std. Err.	W	р
(Intercept)	3.868	1.946	3.95	0.0469
Dietary Diversity (H')	-2.949	0.946	9.71	0.0018
Home range	-14.335	3.518	16.61	4.6e-05
Dietary diversity * HR	7.087	1.685	17.68	2.6e-05
Uric acid	ß	Std. Err.	W	р
(Intercept)	3.67	2.84	1.67	0.20
Dietary Diversity (H')	-0.61	1.62	0.14	0.71
Home range	-9.53	16.16	0.35	0.56
Dietary diversity * HR	-4.59	7.45	0.38	0.54
Total protein	ß	Std. Err.	W	р
(Intercept)	89.39	9.09	96.62	<2e-16
Dietary Diversity (H')	-9.42	6.62	2.02	0.15
Home range	3.92	16.42	0.06	0.81
Dietary diversity * HR	1.59	10.89	0.02	0.88

Supplementary Table 4 (cont.). Generalized estimation equations (GEE) models outcomes for the effect of body condition and dietary diversity, as estimated with the Shannon-Wiener Index (H'), on the biochemical markers of Asian water monitor lizards based on home range size. Home range was estimated using Local Convex Hull and expressed in Km².

	ii uiiu uiipi e			
Albumin	ß	Std. Err.	W	р
(Intercept)	53.80	14.76	13.28	0.00027
Dietary Diversity (H')	-19.54	9.66	4.09	0.04303
Home range	-18.90	28.17	0.45	0.50216
Dietary diversity * HR	14.10	14.10	1.00	0.31744
Globulin	ß	Std. Err.	W	р
(Intercept)	3.4887	0.1641	451.89	<2e-16
Dietary Diversity (H')	0.3109	0.0872	12.72	<0.001
Home range	0.5508	0.4557	1.46	0.22678
Dietary diversity * HR	-0.3451	0.2102	2.69	0.10071
Sodium	ß	Std. Err.	W	р
(Intercept)	136.42	20.07	46.19	1.1e-11
Dietary Diversity (H')	6.27	9.21	0.46	0.50
Home range	3.11	36.15	0.01	0.93
Dietary diversity * HR	2.15	16.69	0.02	0.90
Potassium	ß	Std. Err.	W	р
(Intercept)	3.5130	0.5684	38.20	6.4e-10
Dietary Diversity (H')	0.0535	0.2610	0.04	0.835
Home range	-0.6470	1.0342	0.39	0.530
Dietary diversity * HR	0.1916	0.4769	0.16	0.690
Chloride	ß	Std. Err.	W	Р
(Intercept)	101.31	7.32	191.49	<2e-16
Dietary Diversity (H')	2.32	5.08	0.21	0.65
Home range	-25.25	16.34	2.39	0.12
Dietary diversity * HR	11.58	9.17	1.60	0.21

Supplementary Table 5. Outputs of generalized estimation equation (GEE) on the effect of body condition index and dietary diversity, as estimated with the Shannon-Wiener Index (H'), on the prevalence of each parasite taxonomic group.

Parasite richness (both habitats)							
Variable	ß	Std. Err.	W	р			
(Intercept)	0.0232	0. 5585	0.00	0.97			
Body condition	0.8389	0.9104	0.85	0.36			
Diet diversity (H')	0.0568	0.2395	0.06	0.81			
Parasite richness (forest)							
Variable	ß	Std. Err.	W	р			
(Intercept)	-3.415	2.703	1.60	0.21			
Body condition	-0.451	1.521	0.09	0.77			
Diet diversity (H')	1.922	1.224	2.39	0.12			
Parasite r	richness (oil	palm plantati	on)				
Variable	ß	Std. Err.	Ŵ	p			
(Intercept)	-0.150	0.512	0.09	0.77			
Body condition	2.231	0.739	9.12	0.002			
Diet diversity (H')	-0.357	0.272	1.72	0.19			
Prevalence (overall)							
Variable	ß	Std. Err.	W	р			
(Intercept)	0.998	0.247	16.27	5.5e-05			
Body condition	0.273	0.200	1.86	0.17			
Diet diversity (H')	-0.152	0.119	1.65	0.20			
Ca	<i>pillaria</i> spp. (j	prevalence)					
Variable	ß	Std. Err.	W	р			
(Intercept)	2.497	0.362	47.45	5.6e-12			
Body condition	-0.125	0.113	1.22	0.27			
Diet diversity (H')	-0.289	0.196	2.17	0.14			
O	xyurida spp. (j	prevalence)	***				
Variable	ß	Std. Err.	W	р			
(Intercept)	1.842	0.105	306.08	<2e-16			
Body condition	0.163	0.172	0.90	0.34			
Diet diversity (H')	-0.102	0.126	0.66	0.42			
Phy	saloptera spp.	(prevalence)	***				
Variable	ß	Std. Err.	W	р			
(Intercept)	0.661	0.3284	4.05	0.0442			
Body condition	0.017	0.0611	0.08	0.7774			
Diet diversity (H')	-0.665	0.2529	6.91	0.0086			

Supplementary Table 5 (cont.). Outputs of generalized estimation equation (GEE) on the effect of body condition index and dietary diversity, as estimated with the Shannon-Wiener Index (H'), on the prevalence of each parasite taxonomic group.

Variable B Std. Err. W p (Intercept) -1.029 0.702 2.15 0.14 Body condition 0.159 -0.134 1.42 0.23 Dietary diversity (H') 0.394 0.335 1.39 0.24 Strongylida spp. (prevalence) Variable B Std. Err. W p (Intercept) 1.886 0.435 18.80 1.4e-02 Body condition -0.155 0.241 0.41 0.52 Dietary diversity (H') -0.307 0.213 2.07 0.15 Strongyloides spp. (prevalence) V p (Intercept) 1.709 0.2624 42.39 7.5e-13 Body condition -0.049 -0.0427 1.32 0.251 Dietary diversity (H') -0.374 0.1978 3.59 0.058 Trichuris spp. (prevalence) V p (Intercept) -0.713 0.5582 1.63 0.202 Body condition 0.021 0.1092 0.04<		maa spp.	(prevalence)		
(Intercept) -1.029 0.702 2.15 0.14 Body condition 0.159 -0.134 1.42 0.23 Dietary diversity (H') 0.394 0.335 1.39 0.24 Strongylida spp. (prevalence) Variable ß Std. Err. W p (Intercept) 1.886 0.435 18.80 1.4e-03 Body condition -0.155 0.241 0.41 0.52 Dietary diversity (H') -0.307 0.213 2.07 0.15 Strongyloides spp. (prevalence) Variable ß Std. Err. W p (Intercept) 1.709 0.2624 42.39 7.5e-11 Body condition -0.049 -0.0427 1.32 0.251 Dietary diversity (H') -0.374 0.1978 3.59 0.058 Trichuris spp. (prevalence) Variable ß Std. Err. W p (Intercept) -0.713 0.5582 1.63 <td< th=""><th>Variable</th><th>ß</th><th>Std. Err.</th><th>W</th><th>р</th></td<>	Variable	ß	Std. Err.	W	р
Body condition 0.159 -0.134 1.42 0.23 Dietary diversity (H') 0.394 0.335 1.39 0.24 Strongylida spp. (prevalence) Variable ß Std. Err. W p (Intercept) 1.886 0.435 18.80 1.4e-03 Body condition -0.155 0.241 0.41 0.52 Dietary diversity (H') -0.307 0.213 2.07 0.15 Strongyloides spp. (prevalence) Variable ß Std. Err. W p (Intercept) 1.709 0.2624 42.39 7.5e-17 Body condition -0.049 -0.0427 1.32 0.251 Dietary diversity (H') -0.374 0.1978 3.59 0.058 Trichuris spp. (prevalence) V p (Intercept) -0.713 0.5582 1.63 0.2020 Body condition 0.021 0.1092 0.04 0.850 Dietary diversity (H') 0.594 0.2758	(Intercept)	-1.029	0.702	2.15	0.14
Dietary diversity (H') 0.394 0.335 1.39 0.24 Strongylida spp. (prevalence) (prevalence) p Variable ß Std. Err. W p (Intercept) 1.886 0.435 18.80 1.4e-02 Body condition -0.155 0.241 0.41 0.52 Dietary diversity (H') -0.307 0.213 2.07 0.15 Strongyloides spp. (prevalence) Variable ß Std. Err. W p (Intercept) 1.709 0.2624 42.39 7.5e-11 Body condition -0.049 -0.0427 1.32 0.251 Dietary diversity (H') -0.374 0.1978 3.59 0.058 Trichuris spp. (prevalence) Variable ß Std. Err. W p (Intercept) -0.713 0.5582 1.63 0.202 Body condition 0.021 0.1092 0.04 0.850 Dietary diversity (H') 0.594 0.2758 4.	Body condition	0.159	-0.134	1.42	0.23
Strongylida spp. (prevalence) Variable ß Std. Err. W p (Intercept) 1.886 0.435 18.80 1.4e-02 Body condition -0.155 0.241 0.41 0.52 Dietary diversity (H') -0.307 0.213 2.07 0.15 Strongyloides spp. (prevalence) Variable ß Std. Err. W p (Intercept) 1.709 0.2624 42.39 7.5e-12 Body condition -0.049 -0.0427 1.32 0.251 Dietary diversity (H') -0.374 0.1978 3.59 0.058 Trichuris spp. (prevalence) Variable ß Std. Err. W p (Intercept) -0.713 0.5582 1.63 0.202 Body condition 0.021 0.1092 0.04 0.850 Dietary diversity (H') 0.594 0.2758 4.64 0.031	Dietary diversity (H')	0.394	0.335	1.39	0.24
Variable ß Std. Err. W p (Intercept) 1.886 0.435 18.80 1.4e-02 Body condition -0.155 0.241 0.41 0.52 Dietary diversity (H') -0.307 0.213 2.07 0.155 Strongyloides spp. (prevalence) Variable ß Std. Err. W p (Intercept) 1.709 0.2624 42.39 7.5e-12 Body condition -0.049 -0.0427 1.32 0.251 Dietary diversity (H') -0.374 0.1978 3.59 0.058 Dietary diversity (H') -0.374 0.1978 3.59 0.058 Urtercept) -0.713 0.5582 1.63 0.2022 Body condition 0.021 0.1092 0.04 0.850 Dietary diversity (H') 0.594 0.2758 4.64 0.031	Stron	gylida spp.	. (prevalence)		
(Intercept)1.8860.43518.801.4e-00Body condition-0.1550.2410.410.52Dietary diversity (H')-0.3070.2132.070.15Strongyloides spp. (prevalence)VariableßStd. Err.Wp(Intercept)1.7090.262442.397.5e-11Body condition-0.049-0.04271.320.251Dietary diversity (H')-0.3740.19783.590.058Trichuris spp. (prevalence)VariableßStd. Err.Wp(Intercept)-0.7130.55821.630.202Body condition0.0210.10920.040.850Dietary diversity (H')0.5940.27584.640.031	Variable	ß	Std. Err.	W	р
Body condition -0.155 0.241 0.41 0.52 Dietary diversity (H') -0.307 0.213 2.07 0.15 Strongyloides spp. (prevalence) Variable B Std. Err. W p (Intercept) 1.709 0.2624 42.39 7.5e-11 Body condition -0.049 -0.0427 1.32 0.251 Dietary diversity (H') -0.374 0.1978 3.59 0.058 Trichuris spp. (prevalence) Variable B Std. Err. W p (Intercept) -0.713 0.5582 1.63 0.202 Body condition 0.021 0.1092 0.04 0.850 Dietary diversity (H') 0.594 0.2758 4.64 0.031	(Intercept)	1.886	0.435	18.80	1.4e-05
Dietary diversity (H') -0.307 0.213 2.07 0.15 Strongyloides spp. (prevalence) Variable ß Std. Err. W p (Intercept) 1.709 0.2624 42.39 7.5e-13 Body condition -0.049 -0.0427 1.32 0.251 Dietary diversity (H') -0.374 0.1978 3.59 0.058 Trichuris spp. (prevalence) Variable ß Std. Err. W p (Intercept) -0.713 0.5582 1.63 0.202 Body condition 0.021 0.1092 0.04 0.850 Dietary diversity (H') 0.594 0.2758 4.64 0.031	Body condition	-0.155	0.241	0.41	0.52
Strongyloides spp. (prevalence) Variable ß Std. Err. W p (Intercept) 1.709 0.2624 42.39 7.5e-13 Body condition -0.049 -0.0427 1.32 0.251 Dietary diversity (H') -0.374 0.1978 3.59 0.058 Trichuris spp. (prevalence) Variable ß Std. Err. W p (Intercept) -0.713 0.5582 1.63 0.202 Body condition 0.021 0.1092 0.04 0.850 Dietary diversity (H') 0.594 0.2758 4.64 0.031	Dietary diversity (H')	-0.307	0.213	2.07	0.15
Variable B Std. Err. W p (Intercept) 1.709 0.2624 42.39 7.5e-11 Body condition -0.049 -0.0427 1.32 0.251 Dietary diversity (H') -0.374 0.1978 3.59 0.058 Trichuris spp. (prevalence) Variable B Std. Err. W p (Intercept) -0.713 0.5582 1.63 0.202 Body condition 0.021 0.1092 0.04 0.850 Dietary diversity (H') 0.594 0.2758 4.64 0.031	Strong	<i>yloides</i> spp). (prevalence)		
(Intercept)1.7090.262442.397.5e-13Body condition-0.049-0.04271.320.251Dietary diversity (H')-0.3740.19783.590.058Trichuris spp. (prevalence)VariableßStd. Err.Wp(Intercept)-0.7130.55821.630.202Body condition0.0210.10920.040.850Dietary diversity (H')0.5940.27584.640.031	Variable	ß	Std. Err.	W	р
Body condition -0.049 -0.0427 1.32 0.251 Dietary diversity (H') -0.374 0.1978 3.59 0.058 Trichuris spp. (prevalence) Variable ß Std. Err. W P (Intercept) -0.713 0.5582 1.63 0.202 Body condition 0.021 0.1092 0.04 0.850 Dietary diversity (H') 0.594 0.2758 4.64 0.031	(Intercept)	1.709	0.2624	42.39	7.5e-11
Dietary diversity (H') -0.374 0.1978 3.59 0.058 Trichuris spp. (prevalence) F P P (Intercept) -0.713 0.5582 1.63 0.202 Body condition 0.021 0.1092 0.04 0.850 Dietary diversity (H') 0.594 0.2758 4.64 0.031	Body condition	-0.049	-0.0427	1.32	0.251
Trichuris spp. (prevalence) Variable ß Std. Err. W p (Intercept) -0.713 0.5582 1.63 0.202 Body condition 0.021 0.1092 0.04 0.850 Dietary diversity (H') 0.594 0.2758 4.64 0.031	Dietary diversity (H')	-0.374	0.1978	3.59	0.058
Variable ß Std. Err. W p (Intercept) -0.713 0.5582 1.63 0.202 Body condition 0.021 0.1092 0.04 0.850 Dietary diversity (H') 0.594 0.2758 4.64 0.031	Trici	huris spp. ((prevalence)	,	
(Intercept) -0.713 0.5582 1.63 0.202 Body condition 0.021 0.1092 0.04 0.850 Dietary diversity (H') 0.594 0.2758 4.64 0.031	Variable	ß	Std. Err.	W	р
Body condition 0.021 0.1092 0.04 0.850 Dietary diversity (H') 0.594 0.2758 4.64 0.031					-
Dietary diversity (H') 0.594 0.2758 4.64 0.031	(Intercept)	-0.713	0.5582	1.63	0.202
Ż	(Intercept) Body condition	-0.713 0.021	0.5582 0.1092	1.63 0.04	0.202 0.850
	(Intercept) Body condition Dietary diversity (H')	-0.713 0.021 0.594	0.5582 0.1092 0.2758	1.63 0.04 4.64	0.202 0.850 0.031

Supplementary material

Section 2

Fit of distribution for the biochemical values, body condition and parasite data, by maximum likelihood estimation

Body condition

Summary:

min: 0.03 max: 0.67	median: 0.36
mean: 0.373	sample sd: 0.1.36
sample skewness: 0.105	sample kurtosis: 2.24

Candidates: (Best fit distribution in marked in bold)

Normal	Mean (SE)	Sd (SE)	Loglikelihood	AIC	BIC
Normai	0.373 (0.01)	0.14 (0.01)	114	-223	-217
Commo	Shape (SE)	Rate (SE)	Loglikelihood	AIC	BIC
Gamma	6.34 (0.62)	17.00 (1.73)	108	-212	-206



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Cholesterol

Summary:

min: 0.07 max: 5	median: 1.8
mean: 1.914	sample sd: 0.7739
sample skewness: 0.7021	sample kurtosis: 4.363

Normal	Mean (SE)	Sd (SE)	Loglikelihood	AIC	BIC
Normai	1.91 (0.06)	0.77 (0.04)	-227.9	459.8	466.3
Commo	Shape (SE)	Rate (SE)	Loglikelihood	AIC	BIC
Gamma	5.36 (0.55)	2.8 (0.29)	-228.1	460.2	466.7
Locusti	LogMean	LogSd	Loglikelihood	AIC	BIC
Log normal	0.55 (0.03)	0.49 (0.02)	-254.4	494.8	501.3



Low Density Lipoprotein cholesterol

Summary:

min: 0.1 max: 11.6	median: 1.515
mean: 1.514	sample sd: 1.099
sample skewness: 4.805	sample kurtosis: 44.39

NT - 11	Mean (SE)	Sd (SE)	Loglikelihood	AIC	BIC
Normai	1.51 (0.09)	1.1 (0.06)	-245.2	494.3	500.5
Camma	Shape (SE)	Rate (SE)	Loglikelihood	AIC	BIC
Gamma	2.38 (0.25)	1.57 (0.18)	-201.6	407.3	413.4
Loguomod	LogMean	LogSd	Loglikelihood	AIC	BIC
Log normal	0.19 (0.06)	0.74 (0.04)	-212.5	429.1	435.3



High Density Lipoprotein cholesterol

Summary:

min: 0.1 max: 0.82	median: 0.1
mean: 0.1408	sample sd: 0.106
sample skewness: 4.099	sample kurtosis: 22.28

Commo	Shape (SE)	Rate (SE)	Loglikelihood	AIC	BIC
Gainma	4.04 (0.41)	28.73 (3.13)	235	-466.1	-459.7
Log normal	LogMean	LogSd	Loglikelihood	AIC	BIC
	-2.01 (0.03)	0.42 (0.02)	269.9	-535.8	-529.4
Data	Shape 1	Shape 2	Loglikelihood	AIC	BIC
Beta	2.56 (0.26)	14.74 (1.60)	205.2	-406.4	-400



Triglycerides

Summary:

min: 0.05 max: 20.87	median: 0.44
mean: 1.688	sample sd: 2.935
sample skewness: 3.134	sample kurtosis: 15.45

Commo	Shape (SE)	Rate (SE)	Loglikelihood	AIC	BIC
Gamma	0.520 (0.05)	0.31 (0.04)	-244.4	492.8	499.2
Lognormal	LogMean	LogSd	Loglikelihood	AIC	BIC
Log normal	-0.69 (0.12)	1.6 (0.08)	-219.6	443.2	449.7



Total proteins

Summary:

min: 56 max: 106	median: 78.5
mean: 78.39	sample sd: 8.589
sample skewness: 0.02671	sample kurtosis: 3.306

Candidates: (Best fit distribution in marked in bold)

Normal	Mean (SE)	Sd (SE)	Loglikelihood	AIC	BIC	
	78.39 (0.75)	8.59 (0.53)	-471.2	946.3	952.1	
Commo	Shape (SE)	Rate (SE)	Loglikelihood	AIC	BIC	
Gamma	81.98 (10.07)	1.05 (0.13)	-471.7	947.4	953.1	
Log normal	LogMean	LogSd	Loglikelihood	AIC	BIC	
	4.35 (0)	0.11 (0)	-472.4	948.7	954.5	

Logistic $78.45(0.73)$ $4.83(0.35)$ -471.3 946.5 952.3	Logistia	Location	Scale	Loglikelihood	AIC	BIC
70.15 (0.75) 1.05 (0.55) 171.5 910.5 952.5	Logistic	78.45 (0.73)	4.83 (0.35)	-471.3	946.5	952.3





Q-Q plot



1.0

0.8

0.6 CDF

0.4

0.2

0.0

60

70



Albumin

Summary:

min: 10 max: 34	median: 26
mean: 25.93	sample sd: 3.589
sample skewness: -1.849	sample kurtosis: 9.817

Normal	Mean (SE)	Sd (SE)	Loglikelihood	AIC	BIC	
	25.93 (0.31)	3.59 (0.23)	-356	716	721	
Commo	Shape (SE)	Rate (SE)	Loglikelihood	AIC	BIC	
Gamma	38.79 (4.75)	1.50 (0.18)	-374.5	752.9	758.7	
Lagrand	LogMean	LogSd	Loglikelihood	AIC	BIC	
Log normal	3.24 (0.01)	0.18 (0.01)	-386	776.1	781.9	



Globulin

Summary:

min: 36 max: 100	median: 53
mean: 52.58	sample sd: 7.569
sample skewness: 1.665	sample kurtosis: 13.16

	Mean (SE)	Sd (SE)	Loglikelihood	AIC	BIC	
Inormal	52.58 (0.66)	7.57 (0.46)	-454.47	912.95	918.71	
Commo	Shape (SE)	Rate (SE)	Loglikelihood	AIC	BIC	
Gainina	52.15 (6.40)	0.99 (0.12)	-448.49	900.99	906.76	
Log normal	LogMean	LogSd	Loglikelihood	AIC	BIC	
	3.95 (0.01)	0.14 (0)	-446.96	897.92	903.68	



Uric acid

Summary:

min: 0.1 max: 2.42	median: 0.55
mean: 0.6071	sample sd: 0.3212
sample skewness: 1.461	sample kurtosis: 7.55

Normal	Mean (SE)	Sd (SE)	Loglikelihood	AIC	BIC
	0.61 (0.02)	0.32 (0.02)	-55.5	115	121.6
Gamma	Shape (SE)	Rate (SE)	Loglikelihood	AIC	BIC
	3.81 (0.37)	6.28 (0.65)	-30.81	65.63	72.18
Locusti	LogMean	LogSd	Loglikelihood	AIC	BIC
Log normal	-0.63 (0.04)	0.54 (0.03)	-32.54	69.07	75.63



Sodium

Summary:

min: 136 max: 172	median: 160
mean: 159.9	sample sd: 5.581
sample skewness: -0.6021	sample kurtosis: 4.726

Normal	Mean (SE)	Sd (SE)	Loglikelihood	AIC	BIC
Normai	159.88 (0.48)	5.58 (0.34)	-417.38	838.77	844.55
Commo	Shape (SE)	Rate (SE)	Loglikelihood	AIC	BIC
Gamma	807.32 (98.98)	5.05 (0.62)	-418.44	840.89	846.67
Log normal	LogMean	LogSd	Loglikelihood	AIC	BIC
	5 07 (0)	0.03(0)	-419.04	842.08	847.86



Potassium

Summary:

min: 20.4 max: 58	median: 30.25
mean: 31.12	sample sd: 6.454
sample skewness: 1.721	sample kurtosis: 7.128

Normal	Mean (SE)	Sd (SE)	Loglikelihood	AIC	BIC
Inormal	31.12 (0.58)	6.45 (0.41)	-407.2	818.3	824
Commo	Shape (SE)	Rate (SE)	Loglikelihood	AIC	BIC
Gamma	27.07 (3.42)	0.87 (0.11)	-396.2	796.4	802.1
Lognormal	LogMean	LogSd	Loglikelihood	AIC	BIC
Log normal	3.42 (0.02)	0.19 (0.01)	-392.1	788.2	793.9



Chloride

Summary:

min: 0.1 max: 2.42	median: 0.55
mean: 0.6071	sample sd: 0.3212
sample skewness: 1.461	sample kurtosis: 7.55

Normal	Mean (SE)	Sd (SE)	Loglikelihood	AIC	BIC
	102.68 (0.51)	5.89 (0.36)	-424.5	853	858.8
Commo	Shape (SE)	Rate (SE)	Loglikelihood	AIC	BIC
Gamma	293.64 (35.99)	2.86 (0.35)	-426.7	857.4	863.2
Loomoment	LogMean	LogSd	Loglikelihood	AIC	BIC
Log normal	4.63 (0)	0.06(0)	-428	859.9	865.7



Fit of distribution for parasite richness by maximum likelihood estimation

Candidates: (Best fit distribution in marked in bold)

Poison	Lambda 1.51	S. Error 0.144	AIC 227	BIC 229
Neg himanial	Size (SE)	mu (SE)	AIC	BIC
Neg. binomiai	672.22 (4484)	1.51 (0.144)	229	234



Histogram and theoretical densities Empi

Empirical and theoretical CDFs





Fit of distribution for parasite prevalence by maximum

likelihood estimation

Doison	Lambda	S. Error	AIC	BIC
POISON	2.65	0.062	3060	3070
Neg. binomial	Size (SE)	mu (SE)	AIC	BIC
	0.53(0.04)	2.65 (0.15)	4532	4537

