Beyond the ecology of fear: non-lethal effects of predators are strong whereas those of parasites are diverse

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Abstract

Individuals can alter their behaviour and other traits to reduce threats from predators and parasites. However, predators and parasites likely elicit different responses, which subsequently lead to different non-lethal effects. We created a sequentially structured framework to examine trait responses to distinct predatory and parasitic consumers. We predicted that parasites with strong negative effects on host fitness should act like predators and elicit strong responses before attack. We also predicted that less damaging parasites and micropredators should elicit diverse responses across multiple interaction stages, because their hosts and prey remain alive while being eaten. A meta-analysis indicated that predators do tend to elicit stronger responses than parasites before attack, whereas parasites generally elicit responses after attack, albeit weaker than pre-attack responses to predators. Organisms exposed simultaneously to predator and parasite cues responded similarly when exposed to predator cues alone, suggesting that individuals prioritize anti-predator responses over responses to less harmful parasites. Extending these findings requires addressing knowledge gaps concerning responses to different consumer types, costs of immune responses, and cumulative effects of repeated responses. Expanding research beyond the predator vs. parasite dichotomy toward a broader consumer-resource perspective will facilitate understanding of non-lethal effects in complex, multi-trophic food webs.

Introduction

"Whenever I swim in the ocean… I feel increasingly panicky and … I must leave the water" is a typical response to the 1975 film Jaws (Cantor 2004). As with moviegoers, many species respond to predators by changing behaviours, physiology, or even appearance to avoid being eaten. These non-lethal effects of predators, known as 'trait responses', are pervasive and take many forms, such as seeking shelter (Creel *et al.* 2005) or maturing faster to reach less vulnerable life stages (Raffel *et al.* 2010). Such trait responses influence how individuals interact with the broader community, driving 'trait-mediated effects' that range from reduced individual fitness to trophic cascades (Werner & Peacor 2003; Ritchie & Johnson 2009; Buck & Ripple 2017) that can destabilize communities (Pringle *et al.* 2019). Wolves, for example, frighten elk away from exposed foraging grounds into sheltered habitats with less nutritious vegetation, which then reduces elk birth rates (Creel *et al.* 2007) and alters vegetation structure (Fortin *et al.* 2005). Predators can therefore impact species and communities without directly killing prey, just as *Jaws* kept many people from swimming in the summer of 1975.

Perhaps less well recognised is that parasites also elicit trait responses in hosts with associated non-lethal effects. To reduce infection risk, hosts may avoid infected conspecifics (Milinski & Bakker 1990; Kavaliers *et al.* 2003a; Behringer *et al.* 2006),

68 defend against infectious propagule attack (Sears *et al.* 2013), or avoid risky areas,
69 such as faeces representing a hot spot of undetectable nematode eggs (Hart 1994;
70 Curtis 2014; Weinstein *et al.* 2018). Furthermore, in stark contrast to predation,
71 parasitism is not immediately lethal, so hosts can also respond *after* successful
72 parasite attack through various physiological and behavioural responses (Rigby *et al.*
73 2002; Raberg *et al.* 2009; Buck 2019). For instance, a caterpillar can initiate an
74 immune response to prevent being killed by a parasitoid wasp (Abram *et al.* 2019).
75 Basic emotions like "disgust" (Curtis & de Barra 2018; Tybur *et al.* 2018; Weinstein *et*
76 *al.* 2018) and the age-old cliché "avoid like the plague" suggest that parasite avoidance
77 is interwoven in our own history as much as is our fear of predators. The diverse trait
78 responses elicited by parasites has led some to hypothesize that parasites actually
79 impose stronger cumulative non-lethal effects than predators (Rohr *et al.* 2009; Buck
80 & Ripple 2017).
81 In this review, we compare trait responses to predation and parasitism,
82 considering how they may overlap and differ. Although predators and parasites
83 threaten most species in natural ecosystems, trait responses to predators and
84 parasites have been largely studied in isolation. As a result, how trait responses to
85 parasites compare with trait responses to predators is still unclear. We used a general
86 consumer-resource model to develop hypotheses and predictions for how key life
87 history differences among predators and parasites, such as the number of attacks they

make in a lifetime and whether they kill organisms while eating them, should influence the likelihood and magnitude of trait responses at different interaction stages. We then conducted a systematic review and meta-analysis to: (a) assess the literature that compares trait responses to different forms of predation and parasitism, (b) compare average response magnitudes between predation and parasitism, and (c) test how factors related to resources, consumers, and study designs influence trait responses. We conclude by pointing to several unresolved questions concerning how non-lethal species interactions affect community and ecosystem dynamics.

A general trait-response framework for examining non-lethal effects

Theoretical framework

Predators and parasites employ various 'consumer strategies', that is, how individuals find, attack, and consume organisms (Lafferty & Kuris 2002; Lafferty *et al.* 2015). For example, predators have short feeding times (i.e., seconds to days) and eat multiple organisms in a lifetime, whereas parasites feed on hosts for up to months or even years, but die or transform after a single feeding interaction. Predators kill prey before or while consuming them, but mosquitoes and other micropredators do not. Although some parasites eliminate host fitness, exemplified by parasitoids and parasitic castrators, others infect hosts without substantial fitness impacts. These and other differences in consumer strategies likely affect how, and to what extent,

108 organisms respond to them (Buck 2019). To account for these differences when
109 predicting the non-lethal effects of predation and parasitism, we draw on consumer-
110 resource theory to develop a general trait-response framework that applies across
111 both host-parasite and predator-prey systems.

112 We use, as a scaffolding, the general model for consumer-resource population
113 dynamics developed by Lafferty *et al.* (2015), which collates the key elements of all
114 consumer-resource models into a single, temporally compartmentalized structure
115 (Fig. 1, Box 1). Briefly, predators and parasites are 'consumers', whereas their prey
116 and hosts are 'resources'. Interactions are broken into sequential transitions between
117 up to three discrete consumer states and up to four corresponding resource states
118 (circles in Box 1). State transitions — i.e., mortality, contact, attack failure and success,
119 and feeding (arrows in Box 1) — occur at various rates. Basic differences among
120 consumer – resource systems are incorporated with a set of binary parameters that
121 alter model structure (Box 1).

122 We derive three basic trait responses from the model: **avoid contact, counter**
123 **attack, combat consumption** (Fig. 1)[1]. This temporal sequence implies that trait
124 responses to minimize consumption can be driven by multiple biological mechanisms.

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[1] These classifications are similar to "avoidance", "escape attack", and "escape capture" defined by Lima & Dill (1990) for behavioural responses of prey to predator encounters, though we propose this alternative terminology as a more comprehensive categorization of the diversity of trait responses elicited by different predators and parasites.

125 In initial interactions with *questing* consumers, *susceptible* resources may **avoid**
126 **contact** in various ways. Avoidance serves to reduce the rate that *questing* consumers
127 transition to attacking, with the benefit that *susceptible* resources transition more
128 slowly to *exposed* states (Table 1). Avoidance responses may manifest as trait
129 adaptations [i.e. constitutive responses (Westra *et al.* 2015)], such as camouflaged
130 coloration shown by many species to reduce visibility to predators (e.g. Stevens &
131 Merilaita 2009), or as induced plastic traits, exemplified by herbivores moving away
132 from nematode-infected faeces (Hutchings *et al.* 2001; Weinstein *et al.* 2018) or wolf
133 scents (Creel *et al.* 2005). Resources that become *exposed* to *attacking* consumers may
134 **counter attack** to increase attack failure (Box 1). Countering attack includes "fight or
135 flight" responses, like hares sprinting to burrows when being chased by lynx, or
136 tadpoles jolting their bodies when being attacked by trematode cercariae (Sears *et al.*
137 2013). Finally, resources—particularly hosts of parasites—that become *ingested* may
138 **combat consumption**. Combating consumption shortens or slows consumer feeding
139 rates [i.e. 'resistance' in parasitology (Rigby *et al.* 2002)], or lessens the damage of
140 being eaten [i.e. 'tolerance' in parasitology (Raberg *et al.* 2009)]. Responses that
141 shorten or slow feeding include behaviours like social grooming by primates (Hart &
142 Hart 2018) and adaptive immune responses to parasitism (Hawley & Altizer 2011).
143 Increasing tissue repair and protecting high-risk areas of the body from feeding, as
144 tadpoles do for trematodes (Sears *et al.* 2013), are ways that resources combat

consumption by reducing damage without affecting consumer feeding rates. Whether, and to what degree, resources combat, avoid, or counter, will depend on the different pressures imposed by different consumers, which are modelled by altering rates of contact, attack, and/or consumption. Distinguishing these three model-derived resource trait responses makes it easier to compare, contrast, and make predictions about the different ways that consumers exert non-lethal effects on resources.

Constraints on trait responses

Despite the clear benefits that trait responses provide to resources, various constraints can limit a resource's ability to avoid, counter, and combat its consumers. Hence, predicting the timing and magnitude of trait responses also requires accounting for constraints on resources. Constraints can arise from basic limitations on detecting consumers and mounting responses, or from trade-offs. First, resources can mount responses only if they can detect consumer threats. Resources use visual and non-visual cues to detect predation and parasitism risk, making sensory limitations - e.g., sight, hearing, and smell – a potential constraint on trait responses. Second, resources must possess the morphology, physiology, and energy level to mount specific responses to consumers. For instance, tadpoles cannot physically leave ponds when predators are present as can adult amphibians, so they may instead reduce activity levels to avoid consumer contact (Hossie *et al.* 2017). Third, because

165 trait responses can compete with essential activities like feeding, reproducing, or
166 maintenance (Dröge *et al.* 2017; Hart & Hart 2018), trade-offs can also constrain
167 resource responses. For example, moose can afford to avoid wolves more in summer
168 than in winter when food is scarce (Oates *et al.* 2019). These three constraints likely
169 interact to jointly influence response timing and magnitudes. For example, food
170 scarcity may interact with moose body size or background nutritional levels to
171 determine their ability to avoid contact with wolves. Considering these constraints,
172 along with the potential benefits of response, leads to several hypotheses and
173 associated predictions for how resources should respond to different consumer
174 threats.
175
176 *Hypotheses and predictions concerning trait responses against predators and parasites*
177 **Hypothesis 1: Severe fitness consequences of consumption will favour strong**
178 **trait responses—and strong non-lethal effects—at early interaction stages.**
179 Severe fitness consequences of consumption make combat responses very risky,
180 placing a premium on mounting defensive responses at earlier interaction stages
181 when consumers are questing or attacking. This leads to the intuitive prediction that
182 predators should elicit strong avoidance and counter responses because successful
183 predation leads to death. Perhaps less intuitively, this hypothesis also leads to the
184 prediction that parasitoids, which regularly kill their hosts (Lafferty & Kuris 2002;

185 Abram *et al.* 2019), and parasitic castrators, which reproductively kill their hosts, will
186 be similar to predators in eliciting strong responses at the two early interaction stages.
187 Other types of parasites with strong negative fitness impacts, such as certain
188 pathogens, may place similar pressures on hosts by producing detrimental infections.
189 In contrast, micropredators and less harmful parasites should elicit the weakest
190 avoidance and counter responses of all consumer types.
191
192 **Hypothesis 2: Resources that remain alive while being eaten can implement and**
193 **concentrate responses—and incur non-lethal effects—during consumption.**
194 In stark contrast to most prey of predators, hosts are alive while parasites feed, and
195 prey are alive when micropredators feed. Those resources can therefore mount
196 combat responses while being ingested. This leads to the prediction that, compared to
197 predators, many parasites and micropredators will evoke more types of responses
198 with a more even distribution among the three interaction stages. Because hosts of
199 castrators and many parasitoids remain alive while being eaten, these predictions
200 apply for these types of parasites as well. A less obvious prediction is that the ability
201 to combat consumption may lead to resources concentrating responses in the third
202 interaction stage for parasites – including parasitoid and parasitic castrators - and
203 micropredators, particularly in cases where constraints or trade-offs limit avoidance
204 and combat responses.

205

206 **Hypothesis 3: Detection ability determines trait response timing and magnitude**.

207 Regardless of the fitness consequences of consumption, an inability to detect questing

208 predators and parasites will preclude mounting avoidance responses. Under this

209 hypothesis, the strength of responses should increase with the ease of detecting

210 consumers. For instance, to the extent that visual detection is important to elicit

211 defensive responses, we predict that resources avoid questing predators more than

212 questing micropredators and parasites, because the generally larger size of questing

213 predators relative to questing micropredators and parasites make them easier to see.

214 Exceptions will exist, however; some parasites have large searching stages (e.g., some

215 hymenopteran wasp parasitoids), which would permit easy detection and subsequent

216 avoidance by hosts. Further, certain predators, like some ambush predators and filter

217 feeders, are actually *not* detectable while questing, but only during attack, which

218 precludes avoiding contact but favours countering attack. Hence, this hypothesis does

219 not predict consistent differences among consumer strategies (e.g. predators,

220 parasites, micropredators, etc.), and could perhaps be most strongly tested using

221 predator and parasite species that span a range of detectability.

222 These three hypotheses are not mutually exclusive and can be integrated to

223 predict how trait responses vary among the different types of predation and

224 parasitism in realistic situations (Fig. 1b-d). For instance, foraging mice will avoid

225 questing owls by hiding in burrows (Fig. 1b). Burrow use may vary with flyover
226 frequency, which predicts mouse-owl contact rates. Burrow use is traded-off against
227 the cost of reducing mouse feeding, and consequently likely depends on mouse
228 nourishment. Mice may also detect infective nematode eggs in feeding fields and then
229 avoid contact by moving to other locations (Fig. 1c). Avoiding contact with nematodes
230 is likely constrained by mouse ability to detect eggs and should also depend on
231 movement costs and food availability in new locations. Unlike avoiding owls, the
232 strength with which mice avoid nematodes may also depend on their ability to combat
233 infection (consumption by the nematode), perhaps by mounting an immune response.
234 Effective immune function would favour mice avoiding substantial avoidance costs
235 (e.g., if mice avoid rich feeding areas with nematodes for poor feeding areas lacking
236 nematodes), which would concentrate non-lethal effects in consumption stages. All
237 three responses may also be expected from caterpillar hosts of wasp parasitoids, with
238 the difference that high risk of death via successful consumption may favour a shift to
239 earlier avoidance and counter responses (Fig. 1d). What remains unclear is whether
240 the broader range of responses, and potential concentration of combat responses, to
241 less virulent parasites like nematodes together might, when combined, rival the
242 magnitude of the avoidance and counter responses to consumers with severe fitness
243 consequences. To compare the overall magnitude of trait responses to parasites and

244 predators, we conducted a systematic review of and meta-analysis on available
245 literature.
246
247 **Systematic review and meta-analysis of trait responses to predation and**
248 **parasitism**
249 We systematically reviewed studies that measured the magnitude of trait
250 responses elicited by predators and parasites. We then performed a meta-analysis on
251 the compiled data to test the predictions established above. Our broad goal with the
252 meta-analysis was to assess how the type and magnitude of trait responses vary by
253 consumer strategy as defined by Lafferty and Kuris (2002): solitary predators,
254 trophically transmitted parasites, typical parasites, and pathogens, parasitoids,
255 parasitic castrators, micropredators, or social predators. Many studies have measured
256 trait responses to predators and parasites alone, but we limited our review to studies
257 that measured comparable responses to both a predator and a parasite for the same
258 resource species. To focus on trait responses conferring defence, we did not consider
259 trait changes originating from general parasite pathology, or from parasite adaptive
260 manipulation of host traits (Poulin *et al.* 1994; Moore 2002; Lafferty & Shaw 2013),
261 though our framework can accommodate such effects.
262 Detailed information about data collection, extraction and analyses are
263 available in the Supplementary Material. Briefly, we compiled 129 entries from 15

264 studies, which included 44 predator-prey interactions, 44 host-parasite interactions,
265 and 41 simultaneous interactions with predators and parasites (Table S1). Although
266 studies measured several morphological, behavioural, and physiological responses,
267 behavioural traits were most common, with activity level being the most reported trait
268 (Fig. S1). No studies fitting our criteria measured physiological or immunological trait
269 responses. The studies spanned the following consumer strategies: solitary predators,
270 trophically transmitted parasites, typical parasites, and pathogens (Table S1). We
271 therefore could not consider responses to parasitoids, parasitic castrators,
272 micropredators, or social predators. Hereafter, we broadly distinguish between
273 predators (i.e. solitary predators) and parasites (i.e. trophically-transmitted, typical, or
274 pathogens). Predator-induced trait responses were only measured during the *questing*
275 predator state (Fig. S1), whereas measurements of parasite-induced responses
276 included questing (10), attacking (9), and consuming (25) states (Fig. S1). There were
277 77 entries for individual-level responses and 49 entries for group-level responses.
278 We calculated the standardized mean difference (Hedge's *d*) (Koricheva *et al.*
279 2013) from included studies as the measure of trait response magnitudes, whereby
280 positive effects denoted reductions in trait values (e.g., reduced activity level or mass),
281 except in measures of space use that measured time in a refuge or distance from a
282 consumer cue (e.g. positive effect would mean an increase in refuge use). We reversed
283 the sign of these values so that positive effect sizes would denote reductions in use of

284 risky habitats, indicative of defence (see Table S1 for further details). Because studies
285 often included a treatment containing both a predator and parasite cue, we also
286 estimated the magnitude of trait responses to the combined presence of predators and
287 parasites. We did not have predictions for how these responses would compare to
288 those made to predators or parasites by themselves. We also considered the following
289 factors related to consumers, resources, and experimental designs that may have
290 influenced response magnitudes: a) the type of trait measured to quantify responses
291 (trait type), b) whether studies used a trait value of individuals or proportions of
292 individuals in group that exhibited the focal trait (analysis scale); c) whether
293 responses were elicited under the physical presence of the consumer, or solely by
294 indirect cues such as used media or ingested conspecifics (consumer presence), d) the
295 genus and species of the consumer and resource, and e) whether the consumer was in
296 a questing, attacking or consuming state (Box 1) when the trait response was
297 measured. We also assessed consumer state and consumer strategy effects using only
298 the parasite data because data on responses to predators were limited to one
299 consumer state (questing) and strategy (solitary predator).
300
301 *Results*
302 We found considerable variation in response magnitude and direction to
303 predators (Fig. 2a), parasites (Fig. 2b), and their combination (Fig. 2c). However,

304 although individual parasite-induced effects were sometimes just as strong as
305 predator-induced effects (Fig. 2), on average and across all stages, predator-based trait
306 responses were stronger than parasite-based trait responses (Table S2, Fig. 3a). These
307 patterns were also evident after controlling for consumer state (i.e., questing
308 predators vs. questing parasites) (Table S2, Fig. 3b). Nevertheless, distinguishing
309 between parasite states (questing, attacking, or consuming) revealed that parasites, on
310 average, did elicit responses, but only while they were consuming (i.e. infecting) their
311 hosts (Table S2. Fig. 3b). The simultaneous presence of predators and parasites also
312 elicited responses on average, and they were similar in magnitude to trait responses
313 elicited by predators alone ($z = 0.10$, $p = 0.476$; Fig. 3a). Predators and the
314 simultaneous presence of predators and parasites elicited reductions in activity but,
315 on average, did not influence space use or morphological/physiological traits (Table
316 S2, Fig. 3c). Whether traits were measured at the individual level or group level (e.g.
317 proportions) influenced response magnitudes, with group-level responses being
318 stronger (Table S2, Fig. d). Responses were not contingent on the consumers being
319 physically present; indirect cues of the consumers elicited similar responses (Table
320 S2). Across the host-parasite interactions studied, responses did not depend on the
321 specific strategy of parasites (pathogens, trophically transmitted parasites, or typical
322 parasites; Table S2), and there was insufficient replication to consider how consumer

323 or resource taxon influenced responses. For that reason, these results mostly pertain

324 to amphibians as resources (Table S1).

325

326 **Discussion**

327 We used a general consumer-resource model to construct a framework that can

328 be broadly applied across many predator-prey and host-parasite systems to predict

329 trait responses and non-lethal effects. The framework identified plausible

330 mechanisms driving the timing and magnitude of trait responses, including the fitness

331 consequences associated with being eaten, whether individuals are alive while being

332 eaten, and the ease of detecting consumers. From these hypothesized mechanisms, we

333 generated testable predictions regarding how trait responses should differ between

334 predator-prey and host-parasite interactions. We generally predict severe fitness

335 consequences of predator consumption to drive strong avoidance and counter

336 responses in prey before any contact is made. We also predict that, in general, host

337 responses to parasites are weaker than those of prey, but also more diverse; a range of

338 behavioural, morphological, and physiological responses can be made throughout all

339 interaction stages (Rigby *et al.* 2002; Raberg *et al.* 2009), and potentially concentrated

340 to combat consumption. These general predictions were supported by our meta-

341 analysis on the existing literature to directly compare trait responses to predatory

342 versus parasitic consumers. However, the meta-analysis data predominantly related

343 to a rather narrow taxonomic range of predators and parasites, and several limitations
344 of the included studies (Box 2) suggest ways forward to corroborate and expand the
345 results.

346 Several overlooked distinctions in how organisms respond to parasites likely led
347 to underestimation of overall response magnitudes to parasitism in our meta-analysis.
348 None of the included studies measured individual responses in more than one
349 interaction stage, even though parasites commonly evoke responses in all interaction
350 stages. Longitudinal data on individual responses to multiple consumer states will
351 more comprehensively quantify trait response magnitudes, and may even reveal
352 interactive effects between trait responses (Boxes 2,3). Given that immunological
353 responses may be the most common type of host response to parasitism, non-lethal
354 effects arising from host combat responses, in particular, are likely to be much
355 stronger than our meta-analysis suggests. Additionally, non-lethal effects of parasitism
356 can also arise from host phenotypic changes caused by parasite manipulation (Poulin
357 *et al.* 1994; Lafferty & Shaw 2013), and even directly from parasite feeding
358 independent of defensive responses. For instance, general energy drain (Munger &
359 Karasov 1989; Delahay *et al.* 1995) or direct tissue damage caused by parasite
360 infection can substantially impact host performance (Palstra *et al.* 2007). Such
361 pathological effects are not driven by a host response, but nevertheless represent non-
362 lethal effects. These distinct types of non-lethal effects of parasitism could collectively

363 rival in magnitude the stronger predator avoidance that we observed. To test this
364 hypothesis would require longitudinal data on predator responses as well, which our
365 review indicates is also lacking in the literature. Although we expect combat
366 responses to predation to be rare, there are exceptional cases of prey defending
367 themselves while being ingested, particularly for some slow predators that do not kill
368 their prey before consuming them (e.g., sea stars eating mussels). In such cases,
369 predators could also evoke combat responses.

370 Considering distinct predator and parasite consumer strategies led to more
371 comprehensive trait response predictions that did not completely align with the
372 predator versus parasite dichotomy. However, our systematic review revealed a
373 paucity of literature to develop this more holistic approach at understanding trait
374 responses, suggesting a fruitful area of future research on non-lethal effects. For
375 example, we predict parasitoids and parasitic castrators should act like predators to
376 elicit strong pre-contact responses, but share with other parasites the ability to elicit
377 combat responses during consumption. Micropredators, by not killing their prey when
378 feeding, should act like parasites to elicit responses across all interaction stages.
379 Studies that focus solely on micropredators (Kavaliers *et al.* 2003b, 2005) and
380 parasitoids (Abram *et al.* 2019), do find that resources avoid, counter, and combat
381 these consumers, though we still lack direct comparisons of the magnitudes of these
382 responses with similar responses to predators and typical parasites. Furthermore

383 there remains much to be known regarding the extent to which detectability
384 constrains or enables responses. Testing these more specific, yet meaningful, trait
385 response predictions requires distinguishing not just between predators and
386 parasites, but also different types of predators and parasites. A synthesis of trait
387 responses from multiple single-consumer studies may permit tests of these
388 predictions, but will come with the potential expense of error from inconsistent study
389 designs. To minimize such error, we encourage experiments that directly compare
390 trait responses to a broader range of consumer strategies and resource species.
391 Regardless of how individual resources respond to predators and parasites
392 alone, risks of predation and parasitism in the wild rarely occur in isolation. The non-
393 additive predator and parasite effects that we observed in the meta-analysis may be
394 indicative of priority effects, whereby the first type of exposure elicits the stronger
395 response, though we could not test for this. Additionally, predators may frequently
396 interfere with parasite responses by imposing stronger immediate threats to survival.
397 Trade-offs between defences against predation and parasitism, such as adjustments in
398 activity by tadpoles (Koprivnikar & Urichuk 2017) and shoaling behaviour by guppies
399 (Stephenson *et al.* 2015), could also explain why it might be difficult to respond
400 effectively to different simultaneous threats. However, although trade-offs between
401 predator and parasite defences have been considered previously (Orlofske *et al.* 2012;
402 Stephenson *et al.* 2015; Koprivnikar & Urichuk 2017), our meta-analysis highlights

403 that anti-predator and anti-parasite responses may also be complementary in that
404 predators and parasites can elicit similar responses, and most of the significant
405 predator and parasite responses reported by studies were in the same direction (i.e. a
406 reduction in the trait expression). A well-demonstrated example comes from tadpoles
407 (Box 3), which reduce activity levels (Marino *et al.* 2014; Preston *et al.* 2014; Gallagher
408 *et al.* 2019), increase refuge use (Han *et al.* 2011) and reduce time in foraging habitats
409 (Koprivnikar & Penalva 2015) when either exposed to predators or infected with
410 parasites. When responses deter both predators and parasites, avoiding predation
411 may also inadvertently aid in the avoidance of parasites.
412
413 **Conclusion**
414 Whether through fear or through infection, consumers elicit costly trait
415 responses in their resources that give rise to non-lethal effects at the level of
416 individuals, communities, and ecosystems. A general consumer-resource model
417 helped to develop a framework to predict trait responses to various consumer types.
418 Owing to differences in consumer strategies that influence when and how strongly
419 they impact resources, we expect different trait responses to different types of
420 predators and parasites, and therefore, different non-lethal effects. However, many
421 consumer strategies have not yet been tested in a comparative fashion. Expanding
422 research of non-lethal interactions beyond the predator vs. parasite dichotomy toward

423 a broader consumer-resource perspective sets the foundation for exploring how non-
424 lethal effects manifest in the complex, multi-trophic food webs found in real
425 ecosystems.
426

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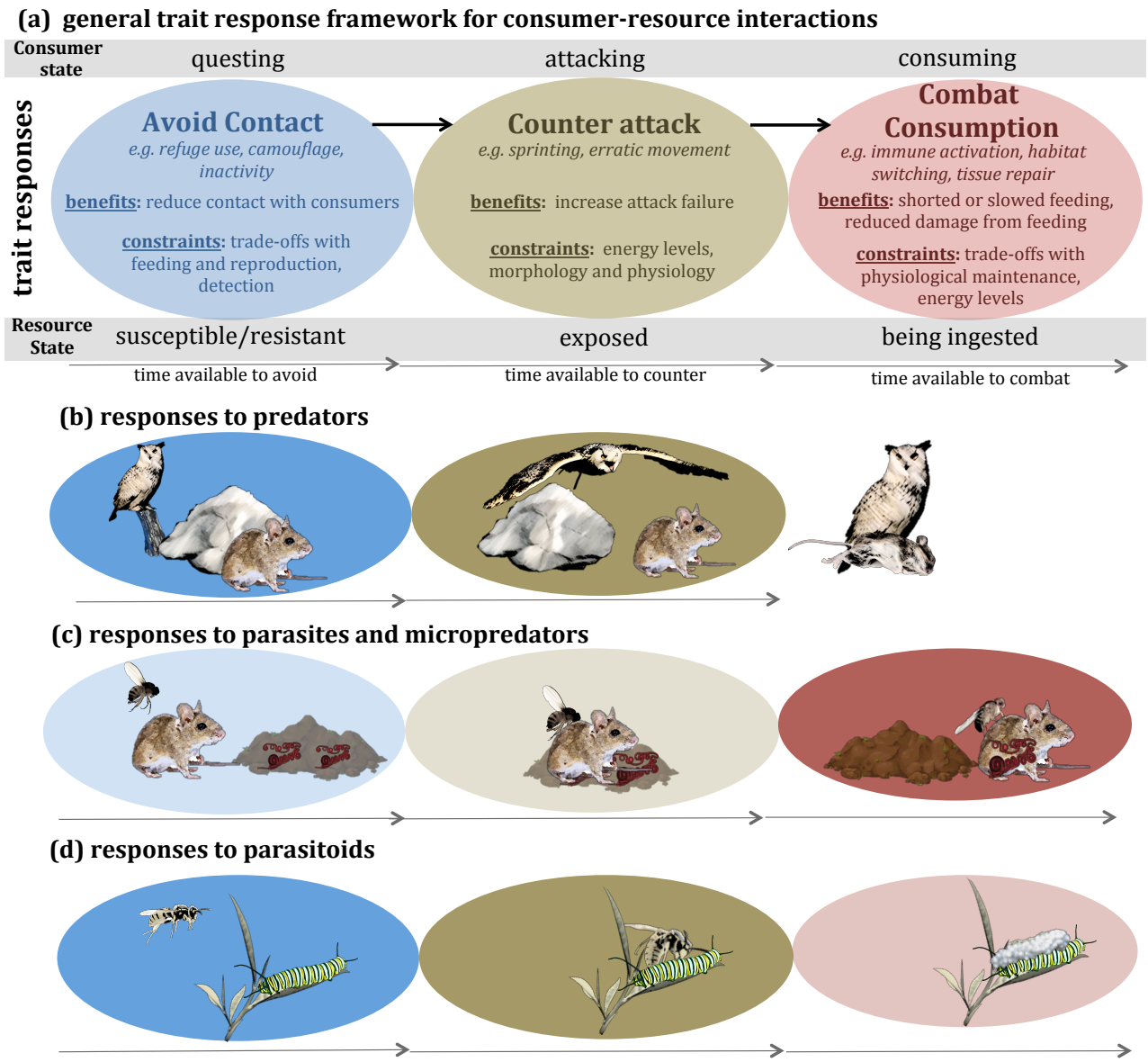

Fig. 1. A general trait response framework and predictions (a) Resources can respond to consumers to reduce contact rates, attack rates, and feeding rates, but might be constrained by physical and sensory limitations, as well as trade-offs against other fitness-related activities (e.g. feeding and reproducing). The general framework can be tailored to specific types of consumer-resource interactions, such as interactions between field mice and **(b)** owl predators, **(c)** biting flies and infective

nematodes (red worms in faeces), or **(d)** between caterpillars and parasitoid wasps. The opacity of the circles denotes the predicted strength of responses. The lack of a combat stage in **(b)** illustrates that resources rarely repond during consumption by predators.

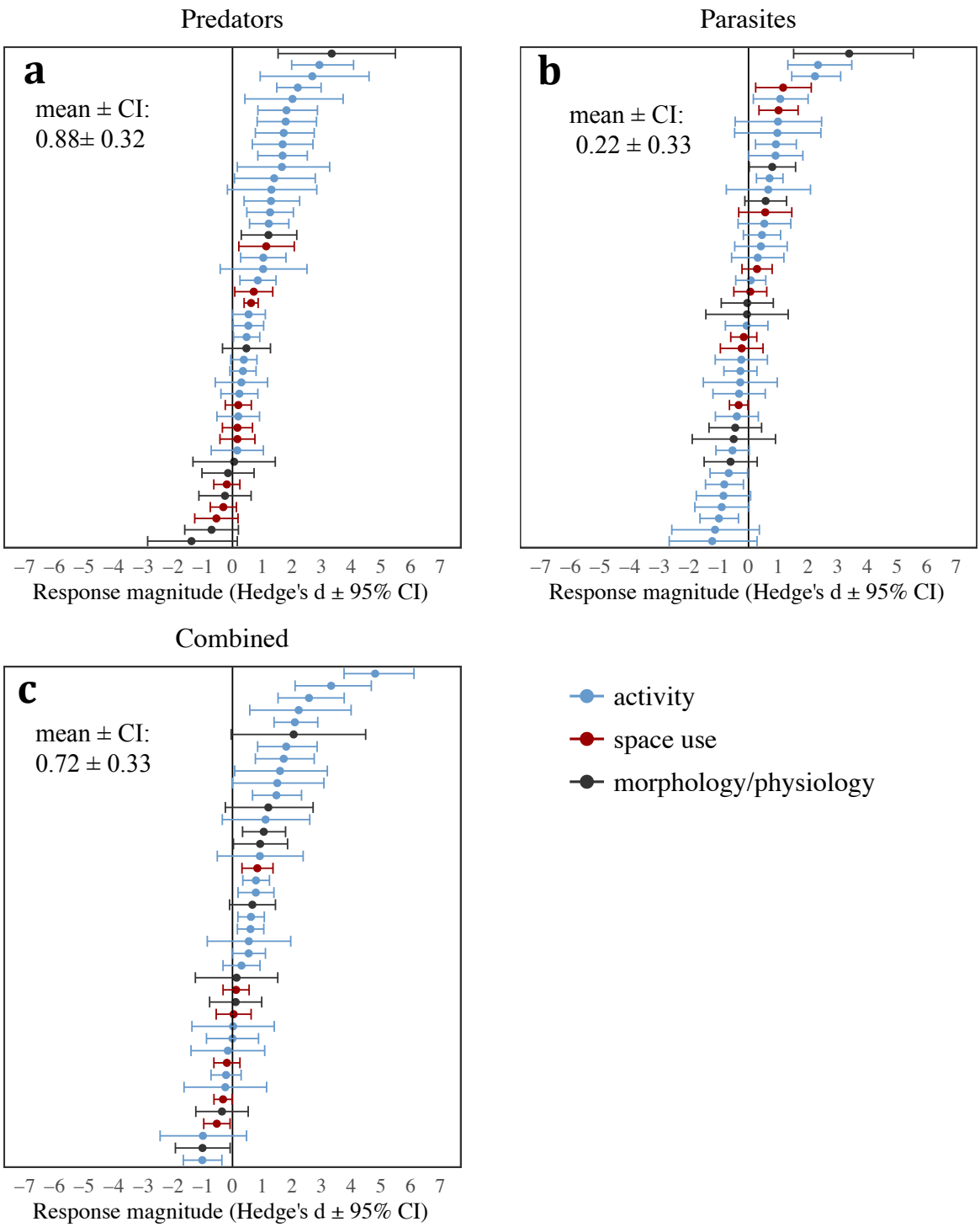

Fig. 2. Forest plots of studies used in the meta-analysis. The distribution of effect sizes for responses elicited by the presence of **(a)** predators, **(b)** parasites, and **(c)** their combined presence resulting from resource adjustments in behavioural (grey)

598 and morphological/physiological traits (blue). Error bars denote the 95% confidence

599 intervals.

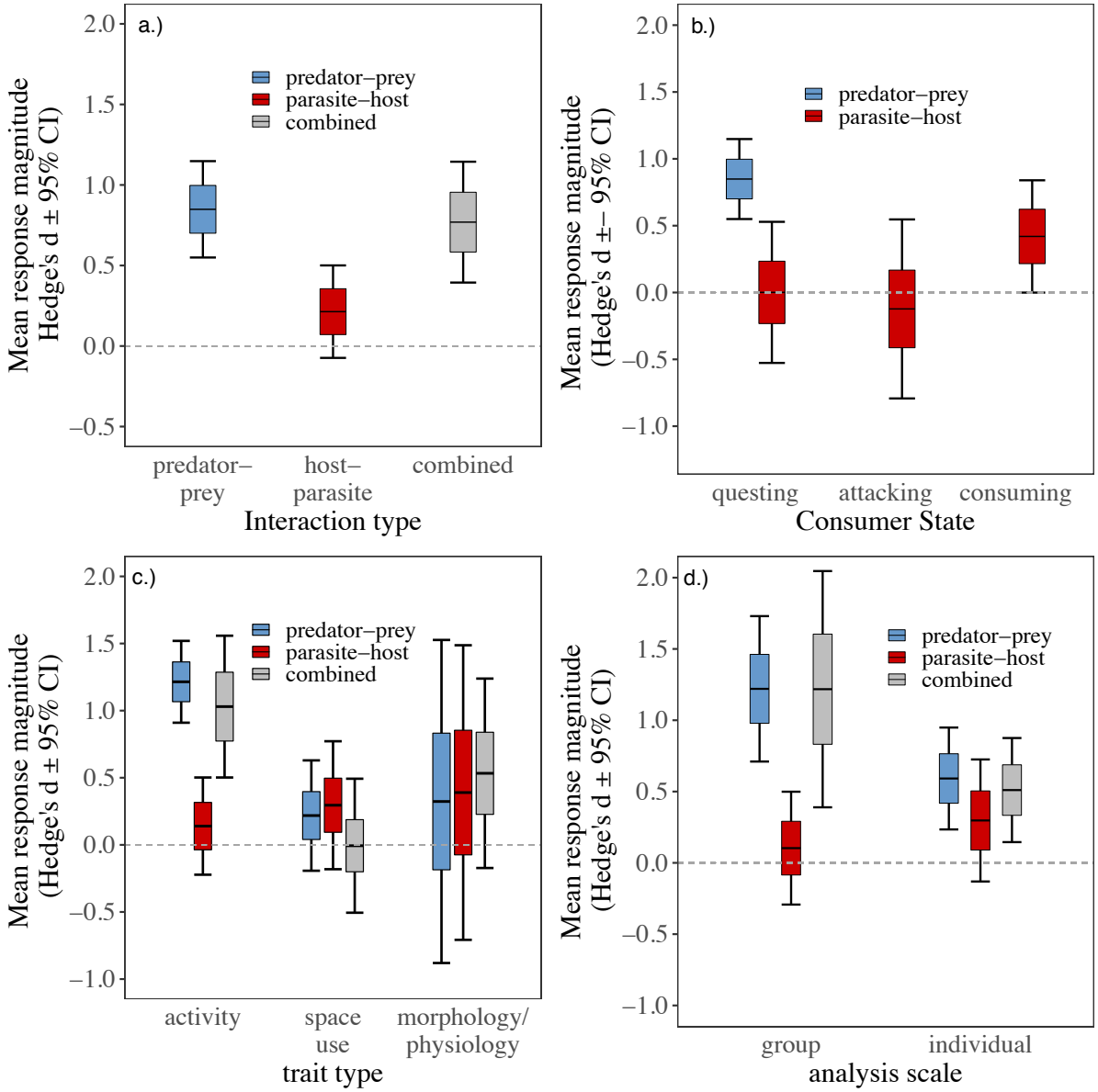

Fig. 3. Relative magnitude of responses to predation vs. parasitism. (a) The estimated mean magnitude of trait responses to predation cues (blue), parasitism cues (red), and both cues (grey). **(b)** Mean trait responses to predators (blue) and parasites (red) during each consumer state comprising the interaction. Only pre-attack responses to questing predators were found in our literature review, likely owing the low probability of surviving attack or consumption by predators. Responses to the combined presence of predators and parasites are not shown because only one study

608 with this treatment had predators and parasites in the same state. **(c, d)** Estimated
609 mean trait response magnitudes to predation cues (blue), parasitism cues (red), and
610 both cues (grey), broken down by **(c)** the type of trait measured and **(d)** the scale at
611 which trait responses measured. Lines denote the mean response magnitudes, boxes
612 denote the standard error of the mean, and error bars denote the 95% confidence
613 intervals.

Resource Response	Resource transition	Consumer transition	processes affected	Examples	Consumer Type	Potential costs to resource	Costs to consumer
Avoid Contact	↑S-R	↓ Q-A	Contact	burrow use when predators are present; vaccination from parasitic infection	All	reduced food intake and reproduction	Hunger
	↓S-E	↓ Q-A	Contact	camoflaged morphology of prey, leaving habitats with cues of parasite infestation	All	reduced food intake and reproduction	energy loss, hunger
Counter attack	↑E-S	↑A-Q	Attack failure Resource Recovery S	Fleeing from approaching predators	Predator, micropredator	energy loss or allocation trade-offs	energy loss, hunger
	↑E-S	↑A death	Consumer death Resource recovery to S	Deflecting parasitic propagules or micropredators; venemous biting of predators	All	energy loss or allocation trade-offs	Death
	↑E-R	↑A-Q	Attack failure Resource recovery to S	fleeing approaching predators via dispersal to areas outside of consumer distribution	Predator	energy loss or allocation trade-offs	Energy loss, hunger
	↑E-R	↑A death	Consumer death Resource recovery to S	Developing antibodies after deflecting parasitic propagules	All	energy loss or allocation trade-offs	Death, hunger
Combat consumption	↑I-S	↑C-Q	Consumption ended Resource recovery to S	swatting, jolted body movement, posionous flesh	Micropredator	energy loss or allocation trade-offs	Failure,
	↑I-S	↑C death	Consumer Death Resource recovery to S	Grooming, immune activation, habitat switching	Micropredator, parasite	energy loss or allocation trade-offs, reduced food intake and reproduction	Death
	↑I-R	↑C-Q	Consumption ended Resource recovery to S	dispersal to areas outside of consumer distribution	Micropredator	energy loss or allocation trade-offs	Failure, hunger
	↑I-R	↑C death	consumer death Resource recovery to S	Sterile immunity	Pathogens	energy loss or allocation trade-offs	Death, hunger

615 **Table 1. Trait responses and their consequences for consumer-resource**

616 **dynamics.** The three types of trait responses that predators and parasites may elicit

617 (Column 1) have distinct effects on interaction dynamics (columns 2-3), in part

618 because each response affects specific biological processes (Column 3). For columns 2

619 and 3: S = susceptible, E = exposed, I = ingested, R = resistant, Q = questing, A =

620 attacking, C = consuming, as per Lafferty et al. 2015. Arrows denote when responses

621 increase transition rates and down arrows denote when trait responses decrease

622 transition rates.

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631 **Box 1. Overview of the general consumer resource model.**

632 The Lafferty *et al.* (2015) model helps identify and compare different consumer-
633 resource interactions using a singular and formalized mathematical logic. During
634 interactions the consumer can be in one of three states: "questing", "attacking", or
635 "consuming". The resource, here being a prey or host, moves through a corresponding
636 four states; they are "exposed" when under attack, being "ingested" while consumers
637 are consuming them, and can either be "susceptible" or "resistant" to new attack. State
638 transitions are driven by multiple biological processes, which can be represented by
639 simple per capita rates or complex functions. Consumers and resources transition
640 from questing and susceptible states, respectively, according to detection rates of each
641 organism and attack rates of the consumer, while they transition to consuming and
642 ingested states, respectively, according to attack success rates of the consumer (Fig.
643 1a). Handling rates determine transitions back to questing and susceptible states or
644 alternatively, death rates of consumers and resources following consumption. All
645 states have death rates that allow for specific costs to be specified. The expanded
646 model shown here can be formally simplified (through setting some rates to zero to
647 subsume states) to represent nearly all classic consumer-resource models.

648 The expanded model does not represent a specific consumer-resource interaction.
649 Instead, a set of binary parameters (switches) makes it easy to specify distinct
650 consumer strategies. For instance, the "fatal attack" parameter (f) defines whether

resources are dead (f = 1) or alive (f = 0) after consumption, which distinguishes predators and parasitoids from other parasites and micropredators. The “joint death” parameter defines whether the consumer dies if its resource dies (j = 1) or remains living (j = 0), which distinguishes all parasites (which have an intimate relationship with their host) from predators and micropredators. Finally, the “multiple attacks” parameter defines whether the consumer attacks once in a lifetime (m = 0), as parasites and parasitoids do, or more than once in a lifetime (m = 1), as micropredators and predators do.

664 **Box 2. Future directions for research on non-lethal effects**

665 There remain several limitations in the comparative data on trait responses to, and
666 non-lethal effects of, predators and parasites. Addressing the following limitations will
667 lead to more comprehensive estimates of non-lethal effects in diverse, real
668 ecosystems:

669 **1. Comparative experiments of trait responses that cover a broader range of**
670 **consumer-resource systems** can determine how generalizable patterns are across
671 systems, and opens avenues to consider factors, like phylogenetics of consumer and
672 resource, on response magnitudes. Most comparative trait response studies identified
673 by our systematic review used larval amphibians and their aquatic consumers. The
674 experimental designs of those studies provide examples of how comparisons of trait
675 responses to different types of consumers can be performed with other species to test
676 the generality of our meta-analysis results.

677 **2. Comparative studies that include responses to parasitic castrators,**
678 **parasitoids and micropredators** are needed to provide novel tests of the
679 mechanisms, such as detection and fitness consequences, underlying trait responses to
680 consumer threats (see Discussion). Comparisons of trait responses to different
681 consumer types are currently limited to typical and trophically-transmitted parasites,
682 pathogens, and solitary predators – only three of the 10 consumer life histories found
683 in natural ecosystems (Lafferty & Kuris 2002; Lafferty *et al.* 2015).
684 **3. Considering the full array of parasite non-lethal effects on hosts** will be
685 important to truly compare predators and parasites. For instance, though immune
686 responses are one of the most common forms of anti-parasite defence, we were not
687 able to include immune responses into comparisons of trait responses to predators
688 and parasites. Because immune responses can be costly to initiate and maintain, such
689 host responses certainly cause non-lethal effects. Further, parasites may alter host
690 traits in ways that do not involve defensive responses, including by pathological
691 energy drain or tissue damage, or via adaptive host manipulation of host phenotypes.
692 All these effects occur during the consumption phase and will be uniquely pronounced
693 for parasites compared to predators.
694 **4. Longitudinal data on prey and host responses** are needed to consider how
695 multiple responses elicited by single consumers collectively shape the magnitude of
696 non-lethal effects. Longitudinal data may even reveal interactive effects between trait

responses, such that mounting one type of response affects the strength of other responses. For example, parasites whose infections are not highly costly (e.g., many gastrointestinal helminths) may cause hosts to prioritize combat responses to minimize trade-offs of avoiding contact against fitness-related activities, like feeding and reproducing (Moore 2002; Hart & Hart 2018). This occurrence may explain why newts, for example, do not avoid infective questing parasites in breeding ponds, but infections from those parasites drive the same individuals to leave those ponds (Daversa *et al.* 2018). Prioritization of combat responses to parasitism provides one explanation for our finding that average responses to parasites were strongest after parasites commenced feeding.

5. Linking trait-response magnitudes to trait-mediated effects can provide estimates of how the non-lethal impacts of consumers on individual traits correspond with the their broader impacts on individual fitness, and community and ecosystem dynamics. Future work can extend the length of prey and host monitoring to link trait responses to individual fitness. Mesocosm and field experiments mirroring the experimental designs of the studies in our meta-analysis can introduce primary producers and other species in food webs into the picture, allowing associations between response magnitudes to predators and parasites and trophic flows and cascades to be quantified.

717 **Box 3. Larval anurans as a case study for interactive non-lethal effects of**

718 **predation and parasitism.**

719 The literature on trait responses to consumers is mostly about frogs. Larval anurans

720 (i.e. tadpoles) were the most studied resource species in our meta-analysis (Table S1),

721 and how tadpole behaviour responds to predation risk (Relyea & Werner 1999; Van

722 Buskirk 2001; Hossie *et al.* 2017) and parasitism (Han *et al.* 2011; Preston *et al.* 2014;

723 Gallagher *et al.* 2019) is well-documented for several species. Questing dragonfly

724 larvae cause tadpoles to reduce activity levels in order to avoid contact, a trait

725 response that can reduce rates at which tadpoles are eaten. Similarly, parasitic

726 trematodes can affect tadpole activity, but tadpole responses seem more variable and

727 depend on the parasite state; *questing* trematode cercariae either elicit no change in

728 activity (Preston *et al.* 2014) or increase activity (Rohr *et al.* 2009; Raffel *et al.* 2010),

729 whereas *attacking* cercariae cause strong activity spikes in tadpoles that increase

730 attack failure rates (Sears *et al.* 2013). However, *consuming* trematode states (larval

731 metacercarial stages in tissues) cause tadpoles to reduce activity (Preston *et al.* 2014).

732 The rich literature using this exemplar system offers guidelines for how studies

733 could be designed to quantify non-lethal effects of predators and parasites in other

734 systems. In general, simultaneous interactions with both predators and parasites elicit

735 reductions in activity similar to encounters with predators alone (Fig. 1a). Although

736 this finding suggests that tadpoles prioritize predator avoidance over parasite

737 avoidance, trait responses elicited during these multi-trophic interactions may be
738 more complex. For example, because trematode-induced changes in tadpole activity
739 vary by parasite state, trait responses and their non-lethal effects may vary depending
740 on the order of encounters, otherwise known as priority effects. Being exposed to
741 attacking trematode cercariae during or after encounters with predatory insects poses
742 a clear trade-off between increasing activity to counter cercariae attack and
743 decreasing activity to avoid contact with the predator. Under the hypothesis that
744 severe fitness consequences of consumption will favour strong trait responses
745 (Hypothesis 1 in main text), the tadpoles should sustain reduced activity levels, giving
746 rise to non-lethal effects in the form of increased infection rates and reduced feeding
747 rates (Fig S4a). By contrast, being exposed to attacking cercariae before encounters
748 with predatory insects should first elicit activity increases, followed by reduced
749 activity in individuals that become infected. If a questing predator is then encountered,
750 infections should facilitate contact avoidance of the predator (Fig. S4b). Nevertheless,
751 the possibility exists that encounters with questing predators while being eaten by
752 parasites elicits additive reductions in tadpole activity that give rise to strong non-
753 lethal effects from reduced feeding. These studies underscore how different consumer
754 states can have different non-lethal effects, and highlight how non-lethal effects of
755 predation and parasitism can interact.
756