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

D.R. Daversa[1,2*], R.F. Hechinger[3], E. Madin[4], A. Fenton[1], *et al*.

[1]Institute of Integrative Biology, University of Liverpool, Liverpool, United Kingdom

[2]Institute of Zoology, Zoological Society of London, London, United Kingdom

[3]Scripps Institution of Oceanography, University of California, San Diego, United States of America

[4]Hawai'i Institute of Marine Biology, University of Hawai'i, Kane'ohe, HI 96744, United States of America

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***Corresponding author:** David Daversa, Institute of Integrative Biology, University of Liverpool, Liverpool, United Kingdom; ddaversa@gmail.com

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.

38

39 **Introduction**

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

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

58 defend against infectious propagule attack (Sears *et al.* 2013), or avoid risky areas,
59 such as faeces representing a hot spot of undetectable nematode eggs (Hart 1994;
60 Curtis 2014; Weinstein *et al.* 2018). Furthermore, in stark contrast to predation,
61 parasitism is not immediately lethal, so hosts can also respond *after* successful
62 parasite attack through various physiological and behavioural responses (Rigby *et al.*
63 2002; Raberg *et al.* 2009; Buck 2019). For instance, a caterpillar can initiate an
64 immune response to prevent being killed by a parasitoid wasp (Abram *et al.* 2019).
65 Basic emotions like "disgust" (Curtis & de Barra 2018; Tybur *et al.* 2018; Weinstein *et*
66 *al.* 2018) and the age-old cliché "avoid like the plague" suggest that parasite avoidance
67 is interwoven in our own history as much as is our fear of predators. The diverse trait
68 responses elicited by parasites has led some to hypothesize that parasites actually
69 impose stronger cumulative non-lethal effects than predators (Rohr *et al.* 2009; Buck
70 & Ripple 2017).
71 In this review, we compare trait responses to predation and parasitism,
72 considering how they may overlap and differ. Although predators and parasites
73 threaten most species in natural ecosystems, trait responses to predators and
74 parasites have been largely studied in isolation. As a result, how trait responses to
75 parasites compare with trait responses to predators is still unclear. We used a general
76 consumer-resource model to develop hypotheses and predictions for how key life
77 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,

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

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

We derive three basic trait responses from the model: **avoid contact, counter attack, combat consumption** (Fig. 1)[1]. This temporal sequence implies that trait 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.

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

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

175 Abram *et al.* 2019), and parasitic castrators, which reproductively kill their hosts, will
176 be similar to predators in eliciting strong responses at the two early interaction stages.
177 Other types of parasites with strong negative fitness impacts, such as certain
178 pathogens, may place similar pressures on hosts by producing detrimental infections.
179 In contrast, micropredators and less harmful parasites should elicit the weakest
180 avoidance and counter responses of all consumer types.
181
182 **Hypothesis 2: Resources that remain alive while being eaten can implement and**
183 **concentrate responses—and incur non-lethal effects—during consumption.**
184 In stark contrast to most prey of predators, hosts are alive while parasites feed, and
185 prey are alive when micropredators feed. Those resources can therefore mount
186 combat responses while being ingested. This leads to the prediction that, compared to
187 predators, many parasites and micropredators will evoke more types of responses
188 with a more even distribution among the three interaction stages. Because hosts of
189 castrators and many parasitoids remain alive while being eaten, these predictions
190 apply for these types of parasites as well. A less obvious prediction is that the ability
191 to combat consumption may lead to resources concentrating responses in the third
192 interaction stage for parasites – including parasitoid and parasitic castrators - and
193 micropredators, particularly in cases where constraints or trade-offs limit avoidance
194 and combat responses.

Hypothesis 3: Detection ability determines trait response timing and magnitude. Regardless of the fitness consequences of consumption, an inability to detect questing predators and parasites will preclude mounting avoidance responses. Under this hypothesis, the strength of responses should increase with the ease of detecting consumers. For instance, to the extent that visual detection is important to elicit defensive responses, we predict that resources avoid questing predators more than questing micropredators and parasites, because the generally larger size of questing predators relative to questing micropredators and parasites make them easier to see. Exceptions will exist, however; some parasites have large searching stages (e.g., some hymenopteran wasp parasitoids), which would permit easy detection and subsequent avoidance by hosts. Further, certain predators, like some ambush predators and filter feeders, are actually *not* detectable while questing, but only during attack, which precludes avoiding contact but favours countering attack. Hence, this hypothesis does not predict consistent differences among consumer strategies (e.g. predators, parasites, micropredators, etc.), and could perhaps be most strongly tested using predator and parasite species that span a range of detectability.

These three hypotheses are not mutually exclusive and can be integrated to predict how trait responses vary among the different types of predation and parasitism in realistic situations (Fig. 1b-d). For instance, foraging mice will avoid

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

234 predators, we conducted a systematic review of and meta-analysis on available
235 literature.
236
237 **Systematic review and meta-analysis of trait responses to predation and**
238 **parasitism**
239 We systematically reviewed studies that measured the magnitude of trait
240 responses elicited by predators and parasites. We then performed a meta-analysis on
241 the compiled data to test the predictions established above. Our broad goal with the
242 meta-analysis was to assess how the type and magnitude of trait responses vary by
243 consumer strategy as defined by Lafferty and Kuris (2002): solitary predators,
244 trophically transmitted parasites, typical parasites, and pathogens, parasitoids,
245 parasitic castrators, micropredators, or social predators. Many studies have measured
246 trait responses to predators and parasites alone, but we limited our review to studies
247 that measured comparable responses to both a predator and a parasite for the same
248 resource species. To focus on trait responses conferring defence, we did not consider
249 trait changes originating from general parasite pathology, or from parasite adaptive
250 manipulation of host traits (Poulin *et al.* 1994; Moore 2002; Lafferty & Shaw 2013),
251 though our framework can accommodate such effects.
252 Detailed information about data collection, extraction and analyses are
253 available in the Supplementary Material. Briefly, we compiled 129 entries from 15

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

risky habitats, indicative of defence (see Table S1 for further details). Because studies often included a treatment containing both a predator and parasite cue, we also estimated the magnitude of trait responses to the combined presence of predators and parasites. We did not have predictions for how these responses would compare to those made to predators or parasites by themselves. We also considered the following factors related to consumers, resources, and experimental designs that may have influenced response magnitudes: a) the type of trait measured to quantify responses (trait type), b) whether studies used a trait value of individuals or proportions of individuals in group that exhibited the focal trait (analysis scale); c) whether responses were elicited under the physical presence of the consumer, or solely by indirect cues such as used media or ingested conspecifics (consumer presence), d) the genus and species of the consumer and resource, and e) whether the consumer was in a questing, attacking or consuming state (Box 1) when the trait response was measured. We also assessed consumer state and consumer strategy effects using only the parasite data because data on responses to predators were limited to one consumer state (questing) and strategy (solitary predator).

Results

We found considerable variation in response magnitude and direction to predators (Fig. 2a), parasites (Fig. 2b), and their combination (Fig. 2c). However,

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

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

314 to amphibians as resources (Table S1).

315

316 **Discussion**

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

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

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

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

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

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

323 generated testable predictions regarding how trait responses should differ between

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

325 consequences of predator consumption to drive strong avoidance and counter

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

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

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

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

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

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

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

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

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

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

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

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

393 that anti-predator and anti-parasite responses may also be complementary in that
394 predators and parasites can elicit similar responses, and most of the significant
395 predator and parasite responses reported by studies were in the same direction (i.e. a
396 reduction in the trait expression). A well-demonstrated example comes from tadpoles
397 (Box 3), which reduce activity levels (Marino *et al.* 2014; Preston *et al.* 2014; Gallagher
398 *et al.* 2019), increase refuge use (Han *et al.* 2011) and reduce time in foraging habitats
399 (Koprivnikar & Penalva 2015) when either exposed to predators or infected with
400 parasites. When responses deter both predators and parasites, avoiding predation
401 may also inadvertently aid in the avoidance of parasites.
402
403 **Conclusion**
404 Whether through fear or through infection, consumers elicit costly trait
405 responses in their resources that give rise to non-lethal effects at the level of
406 individuals, communities, and ecosystems. A general consumer-resource model
407 helped to develop a framework to predict trait responses to various consumer types.
408 Owing to differences in consumer strategies that influence when and how strongly
409 they impact resources, we expect different trait responses to different types of
410 predators and parasites, and therefore, different non-lethal effects. However, many
411 consumer strategies have not yet been tested in a comparative fashion. Expanding
412 research of non-lethal interactions beyond the predator vs. parasite dichotomy toward

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

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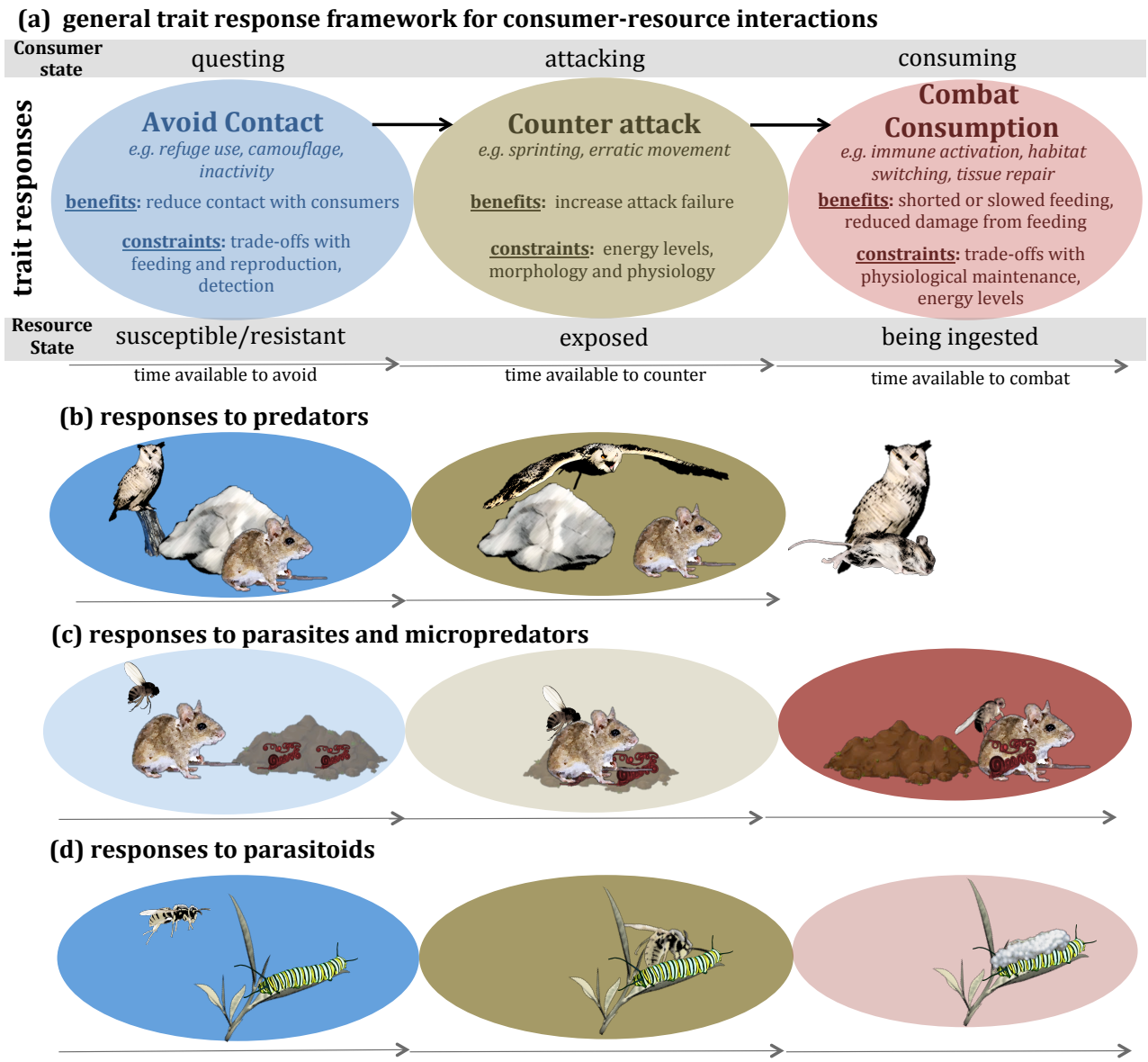

Fig. 1. A general trait response framework and predictions (a) Resources can respond to consumers to reduce contact rates, attack rates, and feeding rates, but might be constrained by physical and sensory limitations, as well as trade-offs against other fitness-related activities (e.g. feeding and reproducing). 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.

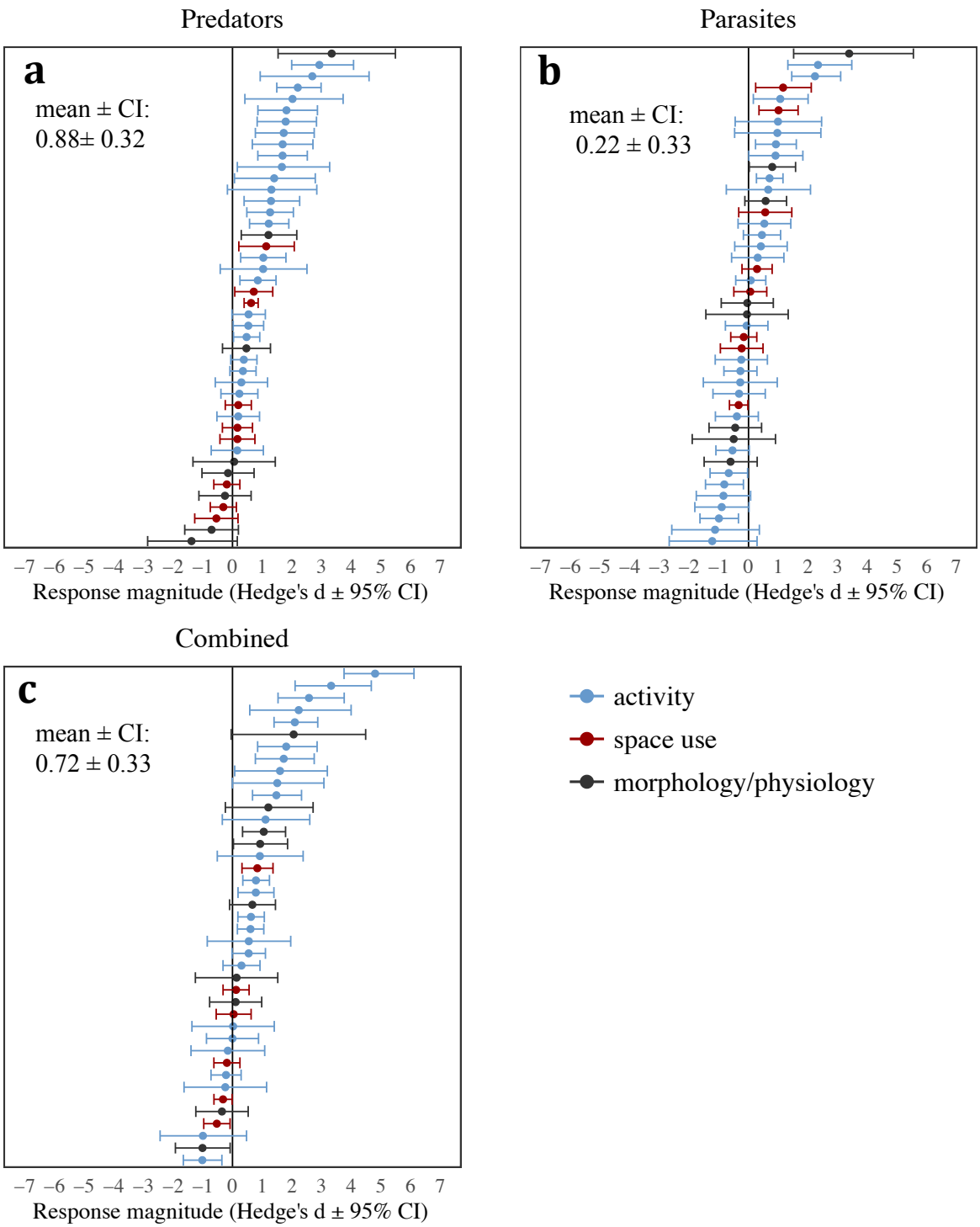

Fig. 2. Forest plots of studies used in the meta-analysis. The distribution of effect sizes for responses elicited by the presence of **(a)** predators, **(b)** parasites, and **(c)** their combined presence resulting from resource adjustments in behavioural (grey)

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

588 intervals.

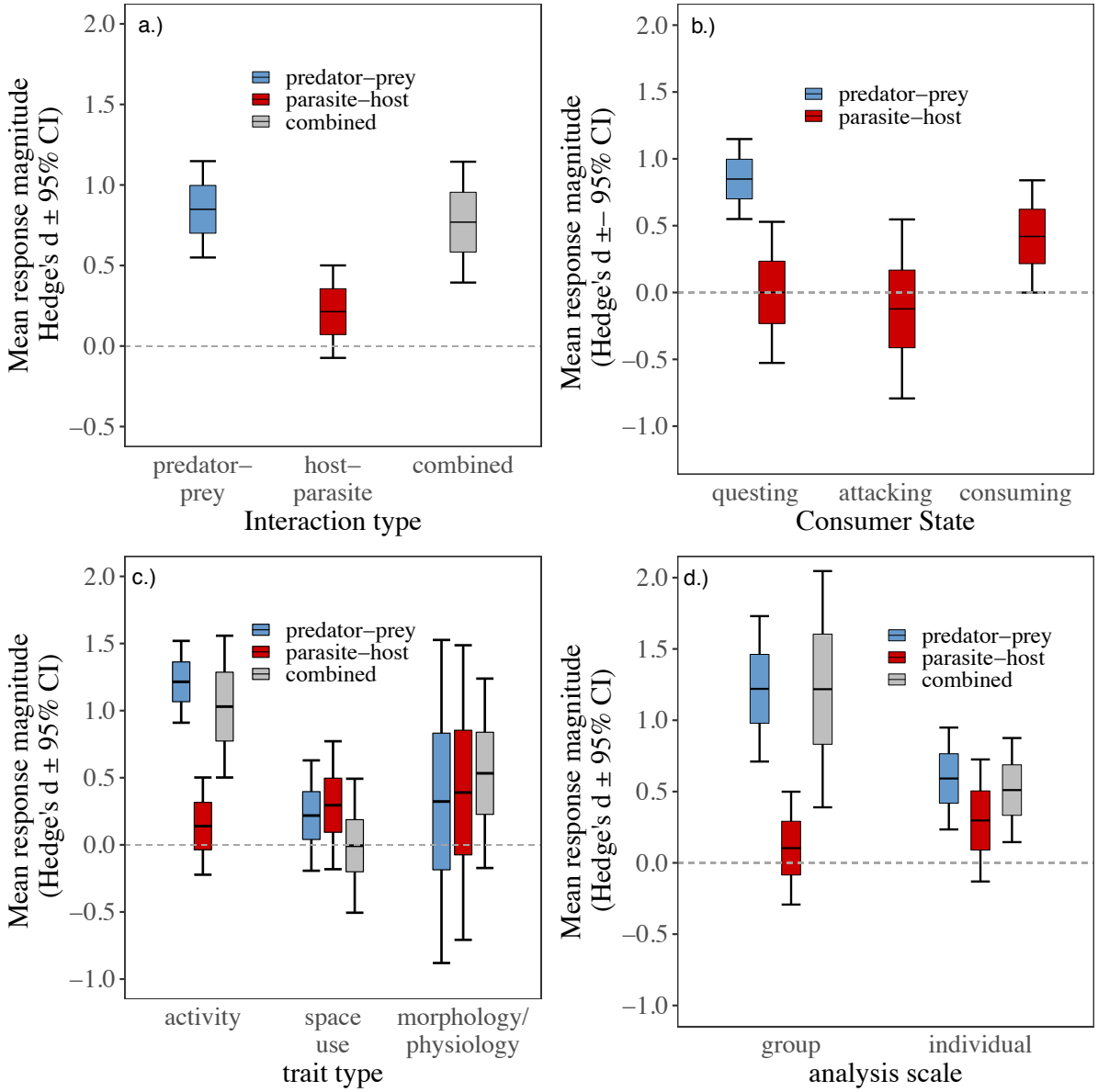

Fig. 3. Relative magnitude of responses to predation vs. parasitism. (a) The estimated mean magnitude of trait responses to predation cues (blue), parasitism cues (red), and both cues (grey). **(b)** Mean trait responses to predators (blue) and parasites (red) during each consumer state comprising the 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

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

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

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

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

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

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

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

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

611 transition rates.

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

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

637 The expanded model does not represent a specific consumer-resource interaction.
638 Instead, a set of binary parameters (switches) makes it easy to specify distinct
639 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.

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

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

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

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

686 responses, such that mounting one type of response affects the strength of other
687 responses. For example, parasites whose infections are not highly costly (e.g., many
688 gastrointestinal helminths) may cause hosts to prioritize combat responses to
689 minimize trade-offs of avoiding contact against fitness-related activities, like feeding
690 and reproducing (Moore 2002; Hart & Hart 2018). This occurrence may explain why
691 newts, for example, do not avoid infective questing parasites in breeding ponds, but
692 infections from those parasites drive the same individuals to leave those ponds
693 (Daversa *et al.* 2018). Prioritization of combat responses to parasitism provides one
694 explanation for our finding that average responses to parasites were strongest after
695 parasites commenced feeding.
696
697 **5. Linking trait-response magnitudes to trait-mediated effects** can provide
698 estimates of how the non-lethal impacts of consumers on individual traits correspond
699 with the their broader impacts on individual fitness, and community and ecosystem
700 dynamics. Future work can extend the length of prey and host monitoring to link trait
701 responses to individual fitness. Mesocosm and field experiments mirroring the
702 experimental designs of the studies in our meta-analysis can introduce primary
703 producers and other species in food webs into the picture, allowing associations
704 between response magnitudes to predators and parasites and trophic flows and
705 cascades to be quantified.

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

707 **predation and parasitism.**

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

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

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

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

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

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

714 response that can reduce tadpole feeding rates. Similarly, parasitic trematodes can

715 affect tadpole activity, but tadpole responses seem more variable and depend on the

716 parasite state; *questing* trematode cercariae either elicit no change in activity (Preston

717 *et al.* 2014) or increase activity (Rohr *et al.* 2009; Raffel *et al.* 2010), whereas *attacking*

718 cercariae cause strong activity spikes in tadpoles that increase attack failure rates

719 (Sears *et al.* 2013). However, *consuming* trematode states (larval metacercarial stages

720 in tissues) cause tadpoles to reduce activity (Preston *et al.* 2014).

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

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

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

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

725 this finding suggests that tadpoles prioritize predator avoidance over parasite

726 avoidance, trait responses elicited during these multi-trophic interactions may be
727 more complex. For example, because trematode-induced changes in tadpole activity
728 vary by parasite state, trait responses and their non-lethal effects may vary depending
729 on the order of encounters, otherwise known as priority effects. Being exposed to
730 attacking trematode cercariae during or after encounters with predatory insects poses
731 a clear trade-off between increasing activity to counter cercariae attack and
732 decreasing activity to avoid contact with the predator. Under the hypothesis that
733 severe fitness consequences of consumption will favour strong trait responses
734 (Hypothesis 1 in main text), the tadpoles should sustain reduced activity levels, giving
735 rise to non-lethal effects in the form of increased infection rates and reduced feeding
736 rates (Fig B3a). By contrast, being exposed to attacking cercariae before encounters
737 with predatory insects should first elicit activity increases, followed by reduced
738 activity in individuals that become infected. If a questing predator is then encountered,
739 infections should facilitate contact avoidance of the predator (Fig. B3b). Nevertheless,
740 the possibility exists that encounters with questing predators while being eaten by
741 parasites elicits additive reductions in tadpole activity that give rise to strong non-
742 lethal effects from reduced feeding. These studies underscore how different consumer
743 states can have different non-lethal effects, and highlight how non-lethal effects of
744 predation and parasitism can interact. Studies that adopt similar experimental designs

in other systems would greatly help broaden out our understanding of resource responses to consumers more generally.