# Broadening the ecology of fear: non-lethal effects arise from diverse responses to predation and parasitism

D.R. Daversa[1,2*], R.F. Hechinger[3], E. Madin[4], A. Fenton[1], A.I. Dell[2,5,6] E. Ritchie[7], J. Rohr[8], V.H.W. Rudolf[9] **

[1] Institute of Integrative Biology, University of Liverpool, Liverpool, United Kingdom
[2]National Great Rivers Research and Education Centre (NGRREC), East Alton, IL, 62024, USA
[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
[5]Department of Biology, Washington University of St. Louis, St. Louis, MO 63130
[6]Dept of Biology, Saint Louis University, Saint Louis, MO 63130
[7]School of Life and Environmental Sciences, Centre for Integrative Ecology (Burwood campus), Deakin University, Geelong, Victoria 3220, Australia
[8]Department of Biological Sciences, University of Notre Dame, Notre Dame, IN, USA
[9]BioSciences, Rice Univ., Houston, TX, USA

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***Corresponding author:** David Daversa; ddaversa@gmail.com

**Not all authors are listed. The full author list will be listed once the paper is published after peer review.

**Abstract**

The ecology of fear demonstrates how prey responses to avoid predation cause non-lethal effects at all ecological scales. Parasites also elicit defensive responses in hosts with associated non-lethal effects, which raises the longstanding, yet unresolved question of how non-lethal effects of parasites compare with those of predators. We developed a framework for systematically answering this question for all types of predator and parasite systems. Our framework predicts that trait responses and their non-lethal effects should be strongest from predators and parasites that do not kill individuals to feed on them, but which nevertheless damage fitness. Analysing trait response data on amphibians, which have been well-studied for this area of research, showed that individuals generally responded more directly to short-term predation risks than to parasitism. Apart from studies using amphibians, there have been few direct comparisons of responses to predation and parasitism, and none have incorporated responses to micropredators, parasitoids, or parasitic castrators, or examined their long-term consequences. Addressing these and other data gaps highlighted by our general framework can advance the field toward understanding how non-lethal effects shape real food webs, which contain multiple predator and parasite species.

## Introduction

Few people watch the movie "Jaws" without experiencing a fear that can make them think twice before swimming in the ocean. Wildlife are no different. Animals avoid foraging

58 where predators are or have been, reduce activity levels, seek refuges, and exhibit other
59 responses in 'fear' of being eaten by predators [1,2]. Fear responses exemplify non-lethal effects
60 of predators on prey traits, and are more generally called 'trait responses'. Trait responses can
61 trigger a broad range of additional non-lethal effects, including 'trait-mediated effects' that
62 range from reduced individual fitness to trophic cascades [3–5] that can destabilize
63 communities [6]. Wolves, for example, frighten elk away from exposed foraging grounds into
64 sheltered habitats with less nutritious vegetation, which then reduces elk birth rates [7] and
65 alters vegetation structure [8]. By eliciting trait responses, predators impact prey, and wider
66 communities, without direct killing.

67 Recent surges in disease outbreaks make clear that parasites also elicit trait responses
68 with non-lethal effects. To reduce infection risk, hosts may avoid infected conspecifics [9–11],
69 defend against infectious propagule attack [12], or avoid risky areas, such as faeces
70 representing a hot spot of undetectable nematode eggs [13–15]. Basic emotions like 'disgust'
71 [15–18] and the age-old cliché "avoid like the plague" suggest that parasite avoidance is
72 interwoven in our own history as much as is our fear of predators.

73 Trait responses to parasites are not confined to avoidance tactics like those made in fear
74 or disgust. Because parasitism is not immediately lethal, hosts can respond, and incur non-lethal
75 effects, after a successful attack by a parasite [19–21]. Immune responses are one of myriad
76 host responses made after infection that can have non-lethal effects [22]. Post-attack trait
77 responses elicited by parasites has led some to hypothesize that parasites cause stronger

78 cumulative non-lethal effects than predators [5,23]. A formal framework for comparing the full
79 range of trait responses to predators and parasites is lacking, however, leaving uncertainty over
80 the similarities and differences in how non-lethal effects accumulate across different predator-
81 prey and host-parasite interactions.

82 Here, we compare trait responses to predation and parasitism, considering how
83 variation in their frequency and strength may drive differences in how non-lethal effects accrue
84 in prey and hosts. Building on recent conceptual developments [21,24], our goal is to establish a
85 quantitative foundation for estimating non-lethal effects in real ecosystems, which contain
86 multiple predator and parasite species. We draw from consumer-resource theory to construct a
87 general framework for estimating trait responses that accounts for the variable consumer
88 strategies of predators and parasites. Unlike current conceptual frameworks for fear and
89 disgust, we deconstruct interactions into sequential phases to consider trait responses before,
90 during, and after an attack, thus allowing us to compare and contrast the complete diversity of
91 predatory and parasitic consumers. We use this framework to form specific predictions
92 regarding how trait responses, and their non-lethal effects, should manifest from interactions
93 with different types of predators and parasites. For brevity, we focus on adaptive trait
94 responses for defence against predation or parasitism, but our framework can also consider
95 maladaptive responses, such as those occurring from parasite manipulation [25]. We then
96 report on a systematic review of the comparative literature on trait responses. We also
97 analysed data on larval amphibians, the most common animal group used by the reviewed

studies, to assess the empirical evidence for our predictions. We conclude by highlighting unresolved questions about trait responses and their non-lethal effects on communities and ecosystems.

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

### *Existing trait response frameworks*

The ecology of fear in predator-prey systems provides a strong, yet incomplete foundation for examining trait responses and their impact on population and community dynamics. 'Fear responses' denote trait responses to the risk of predation, before a predator attack. Prey movement away from foraging habitats when predators are nearby is a well-studied 'fear response' [1,3,26]. As Lima and Dill (1990) pointed out in their seminal framework [1], prey may also exhibit defensive trait responses during predator attack and even after being captured, phases not covered within the standard domain of the 'ecology of fear'. Systematic examination of non-lethal effects must go beyond fear to consider multiple trait responses made throughout interactions. This becomes especially obvious when incorporating responses to parasites.

In stark contrast to predation, host responses after parasite attack, that is, after infection, can continue as parasites feed on individuals. The same is true for prey of micropredators, which act like parasites by feeding without killing. This distinguishing characteristic of host-parasite and micropredator-prey interactions is not factored into the Lima

and Dill (1990) framework, nor it is factored into new conceptual frameworks for disgust [15,24], a form of parasite avoidance. Surviving while being fed on by parasites or micropredators opens up a broad range of responses that slow or stop feeding, or otherwise minimize its impact. Immune responses are a clear example of host responses made during parasite feeding that do not occur in predator-prey systems. Immune responses and other trait responses during parasite and micropredator feeding also cause non-lethal effects to individuals and broader ecosystems [5,21], making their inclusion in systematic examinations of non-lethal effects essential.

*A general trait response framework*

Although trait responses take diverse forms, all responses may be included in our proposed framework (Fig. 1). The framework is informed by a general consumer-resource model [27]. The general consumer-resource model features a single mathematical logic for characterizing the dynamics of all types of host-parasite and predator-prey systems (and other consumer-resource interactions, e.g. decomposer-carcass; plant-pollinator) by breaking down interactions temporally, during which individuals transition through discrete sequential states (Fig. S1). Prey and hosts transition through four states – susceptible, exposed, ingested, resistant (i.e. invulnerable; Fig. S1). For clarity, here we use the term 'consumed' in place of 'ingested'. At the same time, predators and parasites transition through three states - questing, attacking, consuming (Fig. S1). Individuals transition between states following sequential

138 biological processes: contact, attack failure and success, and feeding (further details of the
139 model are provided in the supplementary material).

140 We distinguish three trait response classes in our framework that coincide with the
141 biological processes driving predator-prey and host-parasite interactions: **avoid contact,**
142 **counter attack,** and **combat consumption** (Fig. 1). All three responses can reduce the fitness
143 costs of being consumed, albeit through distinct mechanisms and to varying degrees depending
144 on their efficacy (i.e. the degree of change they cause to the interaction sequence). S*usceptible*
145 prey and hosts may **avoid contact** with *questing* consumers before an attack. Effective
146 avoidance reduces the rate that *questing* predators and parasites transition to *attacking*, and
147 prey and hosts benefit from transitioning more slowly from *susceptible* to *exposed* states (Table
148 S3). Prey and hosts that become *exposed* may **counter attack** to increase the probability that
149 attacks fail. Countering-attack includes "fight or flight" responses, like hares sprinting to
150 burrows when being chased by lynx, or tadpoles rapidly and erratically swimming when being
151 attacked by trematode cercariae [12]. Finally, prey and hosts that are *consumed* (i.e. eaten or
152 infected) and remain alive may **combat consumption**. Combating consumption shortens or
153 slows predator and parasite feeding rates [i.e. 'resistance' in parasitology [19]], or lessens
154 damage from the feeding [i.e. 'tolerance' in parasitology [20]]. Responses that reduce feeding
155 include behaviours like social grooming by primates [28] and adaptive immune responses to
156 parasitism [22]. Increasing tissue repair and protecting high-risk areas of the body from
157 parasite feeding, as tadpoles do in response to trematodes [12], exemplify responses that

158 combat consumption by reducing damage, without affecting feeding rates. Collectively, the
159 combination of three trait responses with two consumer types results in six general pathways
160 for non-lethal effects to arise.
161
162 *Factors shaping the strength, duration, and frequency of trait responses*
163 With the full range of trait responses classified and integrated into consumer-resource
164 dynamics, we can now consider the conditions that determine which responses predators and
165 parasites are likely to elicit, as well as how strong and frequent they are likely to be. The extent
166 to which prey and hosts avoid, counter, and combat consumers depends first and foremost on
167 their basic physical and sensory abilities [29]. For instance, tadpoles cannot physically leave
168 ponds when predators are present. They may, however, reduce activity to avoid contact [30].
169 Individuals must also be able to detect consumer threats to respond to them. Prey and hosts use
170 both visual and non-visual cues to detect predation and parasitism risk, making sensory
171 limitations (e.g. sight, hearing, and smell) potential constraints on trait responses [31,32].
172 Impediments to either risk detection or the ability to act on detected risk should reduce the
173 frequency of trait responses, or even preclude them.
174 Even when prey and hosts have the physical and sensory capacity to mount responses,
175 trade-offs may mediate the frequency and strength of trait responses [29]. The ecology of fear
176 provides ample evidence for the role of trade-offs in shaping trait responses to predators
177 [33,34]. Whether via reductions in foraging, reproduction, or energy levels, fitness-related costs

178 of mounting responses compete with the benefits of responses (i.e. the costs of not responding),
179 making the frequency and strength that individuals exhibit trait responses a matter of
180 economics [29]. An important point not recognized by the ecology of fear (or disgust) is that
181 trade-offs may change over different phases of any given interaction. The frequency, duration,
182 and strength of trait responses will therefore depend not just on their absolute costs but also on
183 the relative costs compared to other possible responses. Exemplified by certain host-parasite
184 interactions, avoiding contact may be more costly than becoming infected, potentially driving
185 stronger and more frequent combat responses after becoming infected. The extent to which
186 'fear' and 'disgust' influence prey and host populations will depend on the feasibility to counter
187 attacks and combat consumption. Phase-specific trade-off situations are accounted for in our
188 framework through functions that link responses to state-specific mortality and fecundity rates,
189 which expresses responses costs. Those costs are balanced by benefits of responses, expressed
190 through response impacts on state transition rates, as described in the above section.
191
192 *Predicting trait responses and non-lethal effects across different predators and parasites*
193 The timing, frequency, and strength of trait responses in prey and hosts will also depend
194 on traits of the predators and parasites, which leads to predictions for how trait responses and
195 non-lethal effects may vary across the different types of consumers. Predators and parasites
196 comprise distinct 'consumer strategies'; that is, basic ways by which individuals feed on and
197 impact other organisms [27,35]. One key difference involves the fitness consequences of

198 predation and parasitism on individual prey or hosts. Predators and most parasitoids eliminate
199 future reproductive success of their prey or hosts by killing them, and parasitic castrators do so
200 by blocking host reproduction. In contrast, feeding by most other types of parasites and
201 micropredators is not so deadly and does not completely eliminate future fitness gains. Given
202 their great risk of consumption, we predict that predators, parasitoids, and parasitic castrators
203 will elicit strong trait responses in their prey and hosts, resulting in overall strong non-lethal
204 effects. Similar patterns may also emerge with other parasites with strong negative fitness
205 impacts, such as highly virulent pathogens, or the micropredators that vector them. However,
206 non-vectoring micropredators and less damaging parasites should elicit relatively weaker
207 responses and weaker associated non-lethal effects. Differences in the fitness consequences of
208 being consumed should then drive variation in non-lethal effects not just between predators
209 and parasites, but also between different types of parasites, with some parasites being more
210 similar to predators than to other types of parasites.

211 We can go further by considering the timing of prey and host death during interactions.
212 Predators usually kill prey before or shortly after commencing to feed. This is not the case for
213 most parasites and their hosts. Even parasitoids and castrators can have a substantial amount of
214 feeding time before hosts are killed or castrated. Recognizing this basic difference in timing of
215 prey and host mortality, or "reproductive death", leads to two clear predictions for how non-
216 lethal effects of predators and parasites differ. First, prey responses to predators will be
217 constrained to avoiding contact and countering attack (Fig. 1b). Second, parasites and

218 micropredators will elicit all three trait responses (Fig. 1c-d), resulting in more diverse non-
219 lethal effects on hosts than prey of predators.
220 Integrating the above hypotheses leads to the prediction that, all else being equal,
221 parasites and micropredators that entail high fitness costs should cause the strongest overall
222 non-lethal effects from trait responses. This includes parasitic castrators, parasitoids, highly
223 damaging pathogens, and the micropredators that vector them. The high fitness costs of feeding
224 by these consumers should drive strong avoidance and counter-responses, resulting in strong
225 non-lethal effects from those responses. Yet, by feeding on living organisms, these consumers
226 also permit combat responses as a source of non-lethal effects, as evidenced in many hosts of
227 parasitoids, parasitic castrators, and other parasites [5,36]. Collectively, we expect non-lethal
228 effects from this triad of trait responses to supersede those arising solely from 'fear' responses
229 (i.e. avoidance of contact and counter of attack) to predators. Exceptions may exist, such as
230 some parasitoids that paralyze hosts during the initial attack, which can make hosts incapable of
231 combatting consumption [36]. On average, however, our framework indicates that non-lethal
232 effects will be strongest not solely from consumers that impose the highest risk of death, but
233 rather from those that impose such strong costs while keeping the consumed host or prey alive.
234

235 **Studies to measure trait responses to predation and parasitism**

236 We reviewed the literature that compares trait responses to predation and parasitism to
237 assess support for our predictions. Specially, we compiled studies that directly compared trait

238 responses to both predation and parasitism risk in a single resource species (see supporting
239 material for details of literature search). The vast majority of studies we found measured trait
240 responses in larval frogs (i.e. 'tadpoles', N = 106 entries across 13 studies, Table S1).
241 Behavioural traits were most common, with activity level being the most reported trait (Table
242 S1, Table S2). We did not find studies that measured immunological trait responses, likely
243 because this is distinct to host-parasite systems. The studies spanned the following consumer
244 strategies: solitary predators, trophically transmitted parasites, typical parasites, and pathogens
245 (Table S1); in no cases were responses to parasitoids, parasitic castrators, micropredators, or
246 social predators considered. Predator-induced trait responses were only measured during
247 *questing* predator states, representing avoidance of contact, whereas measurements of parasite-
248 induced responses included all three states: *questing* (N=9), *attacking* (N=5), and *consuming*
249 (N=24). The limited data we found constrained our ability to make comparisons, although some
250 general patterns did emerge.
251 Analysis of the data on tadpoles, the main animal group used as prey and hosts revealed
252 considerable variation in the magnitude and direction of tadpole responses to predators (Fig.
253 2a), parasites (Fig. 2b), and their combination (Fig. 2c). However, on average and across all
254 consumer and resource states, predator-induced trait responses were stronger than parasite-
255 induced trait responses (Fig. 3a, Table S4). These patterns were evident after controlling for
256 consumer state (comparing questing predators to questing parasites) (Fig. 3b), though they
257 were weaker (Table S4), likely owing to lower power of the data subset. Distinguishing between

258 trait response types (avoid, counter, combat) revealed that tadpoles did respond to parasites,
259 but only by combatting parasites post-infection and at lower magnitudes than their responses
260 to avoid predator contact (Fig. 3b, Table S4). Tadpoles also responded to the simultaneous
261 presence of predators and parasites on average, and at similar magnitudes to their responses to
262 predators alone (Fig. 3a). The strong tadpole responses to predators primarily represented
263 reductions in activity levels (Fig. S7a, Table S4), and they were most evident when measuring
264 group-level responses as opposed to individual-level responses (Fig. S7b, Table S4). Across the
265 host-parasite interactions studied, responses did not differ between pathogens and trophically-
266 transmitted parasites, the two parasite strategies investigated (Table S3).
267
268 **Discussion**
269 Our framework reveals that non-lethal effects from predation and parasitism are a
270 function of diverse and potentially interacting responses by prey and hosts, exhibited at
271 different time points in consumer-resource interactions. The current literature on non-lethal
272 effects provides a very limited portrayal of trait responses, which restrained our ability to test
273 the predictions that emerged from the general framework. Current comparative data comprise
274 brief snapshots of interactions that do not fully capture the temporal dynamics of trait
275 responses (and their non-lethal effects). Longitudinal data that tracks individuals through all
276 interaction phases could provide insight into how non-lethal effects accrue from multiple trait
277 responses. Longitudinal data could also detect interactive effects between trait responses. For

278 example, hosts that invest heavily in immune defences may exhibit weaker avoidance of contact
279 with parasites, particularly if avoidance conflicts with feeding, reproducing, and other fitness-
280 related activities. The growing literature on 'fear' and 'disgust' of parasites, which focuses
281 exclusively on certain forms of parasite avoidance, will benefit by being contextualized within
282 the broader suite of trait responses available to hosts.

283 Trait response data on tadpoles, although limited, underscore the importance of
284 distinguishing nuances in the timing of trait responses. Pooling all trait response measurements
285 suggested that parasites generally did not elicit changes in tadpole activity levels as did
286 predators. However, accounting for response timing revealed significant changes in activity
287 levels that were confined to post-infection periods of interaction. Adult amphibians show
288 similar tendencies to combat infections rather than avoid them [37]. Combat responses appear
289 to be a primary trait response to parasitism in this group of animals, whose role in non-lethal
290 effects can most fully be estimated by treating the responses as separate from those made
291 earlier in interactions.

292 The post-infection combat responses apparent in tadpoles are particularly notable
293 considering that immune responses were not factored in. Immune responses are a very
294 common form of combatting parasitism that can be exhibited for prolonged periods. The
295 combined non-lethal effects of tadpole parasites were therefore likely much stronger than the
296 analysed data suggest. Additionally, non-lethal effects of parasitism could have occurred from
297 host phenotypic changes caused by parasite manipulation [25,38], and even directly from

298 parasite feeding independent of defensive responses. For instance, general energy drain or
299 direct tissue damage caused by parasite infection can substantially impact host performance
300 [39,40]. The diverse sources of non-lethal effects of parasites not relevant to prey collectively
301 could have rivalled in magnitude the stronger predator avoidance observed in tadpoles.

302 Accounting for distinct predator and parasite strategies led to trait response predictions
303 that did not align with the predator versus parasite dichotomy. Pinpointing the sources of
304 variation in non-lethal effects therefore demands a functional approach rather than a taxonomic
305 approach to distinguishing predators and parasites [35]. Parasitoids, and parasitic castrators in
306 particular, could offer rewarding insights because they share functional characteristics with
307 both predators and parasites. Avoidance, counter, and combat responses to parasitoids are
308 well-documented [36], but how their frequency and strength compare with responses to
309 predators and less debilitating parasites is unknown. The latter can also be said for parasitic
310 castrators. Given the high fitness consequences of infection from parasitoids and castrators,
311 together with infections that are not immediately lethal, their combined non-lethal effects may
312 very well be the strongest of all predator and parasite functional groups.

313 Regardless of how individuals respond to predators and parasites alone, risks of
314 predation and parasitism in real ecosystems rarely occur in isolation. Future research could
315 apply our framework to investigate the additive and interactive non-lethal effects of
316 simultaneous exposure to predators and parasites. Our analysis of the tadpole data suggests
317 that responses to simultaneous exposure are non-additive, perhaps owing to the prioritization

318 of responses to the more severe threat (Fig. S5). Although not a focus of this review, evidence
319 for increasing predation of parasitized prey [41–43], and increasing parasitism in predator-rich
320 environments [44], provide further indication that predators and parasites interact to impose
321 non-lethal effects in non-additive ways. Fewer studies have considered single responses that
322 defend against both predators and parasites. Nevertheless, there were several cases where
323 tadpole responses to predators and parasites responses were in the same direction (i.e. a
324 reduction in the trait expression). Trait responses that effectively deter both predators and
325 parasites may mitigate the non-lethal effects incurred from the essential task of defending
326 oneself against being eaten.
327
328 **Conclusion**
329 Whether through fear or through infection, consumers elicit costly trait responses in
330 their resources that give rise to non-lethal effects at the level of individuals, with consequences
331 for communities and ecosystems more generally. A general consumer-resource model helped us
332 to develop a framework for systematically comparing trait responses to various types of
333 predators and parasites. Different types of predators and parasites should elicit different trait
334 responses, and therefore, have different non-lethal effects, given differences in consumer
335 strategies that influence when and how strongly they impact prey and hosts. However, many
336 predator and parasite strategies have not yet been tested comparatively. Expanding research of
337 non-lethal effects to regularly consider different predator and parasite strategies sets the

338 foundation for exploring how non-lethal effects manifest in the multi-dimensional food webs
339 found in real ecosystems.
340

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354

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465

466 **Figures**

467 **Fig. 1. A general trait response framework and predictions. (a)** Resources can mount three
468 sequential responses to consumers, each with distinct effects on the interaction: avoid contact,
469 counter attack, combat consumption. Examples of each type of response are listed in italicized
470 text. Responses may be constrained by physical and sensory limitations, as well as trade-offs
471 against other fitness-related activities (e.g. feeding and reproducing). The general framework
472 can be tailored to specific types of consumer-resource interactions, such as interactions
473 between field mice and **(b)** owl predators, **(c)** biting flies and infective nematodes (red worms
474 in faeces), or **(d)** between caterpillars and parasitoid wasps. The lack of a combat stage in **(b)**
475 illustrates that resources rarely respond during consumption by predators.

476

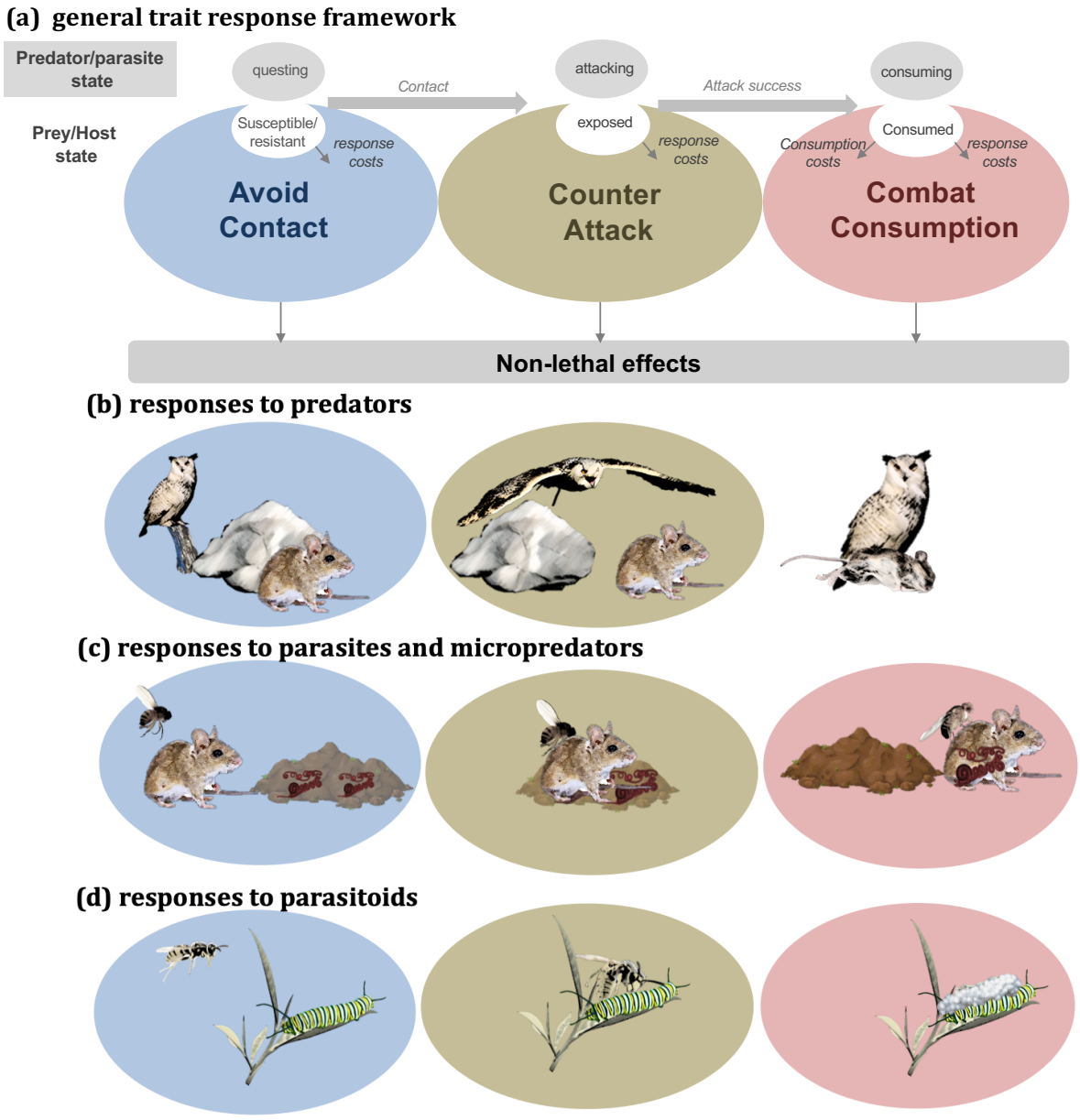
477 **Fig. 2. Forest plots of effect sizes used in the meta-analysis.** The distribution of effect sizes
478 for responses elicited by the presence of **(a)** predators, **(b)** parasites, and **(c)** their combined
479 presence resulting from resource adjustments in activity (blue), space use (red), and
480 morphological/physiological traits (grey). Error bars denote the 95% confidence intervals.

481

482 **Fig. 3. Relative magnitude of responses to predation vs. parasitism. (a)** The estimated mean
483 magnitude of trait responses to predation cues (blue), parasitism cues (red), and both cues (grey).
484 **(b)** Mean trait responses to predators (blue) and parasites (red) when distinguishing by the type
485 of trait responses, as defined in our framework. Only avoidance 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 in **(b)** because only one study with this treatment had predators and parasites in the same state. Lines denote the mean response magnitudes, boxes denote the standard error of the mean, and error bars denote the 95% confidence intervals.

492 Fig. 1




493

494

Fig. 2

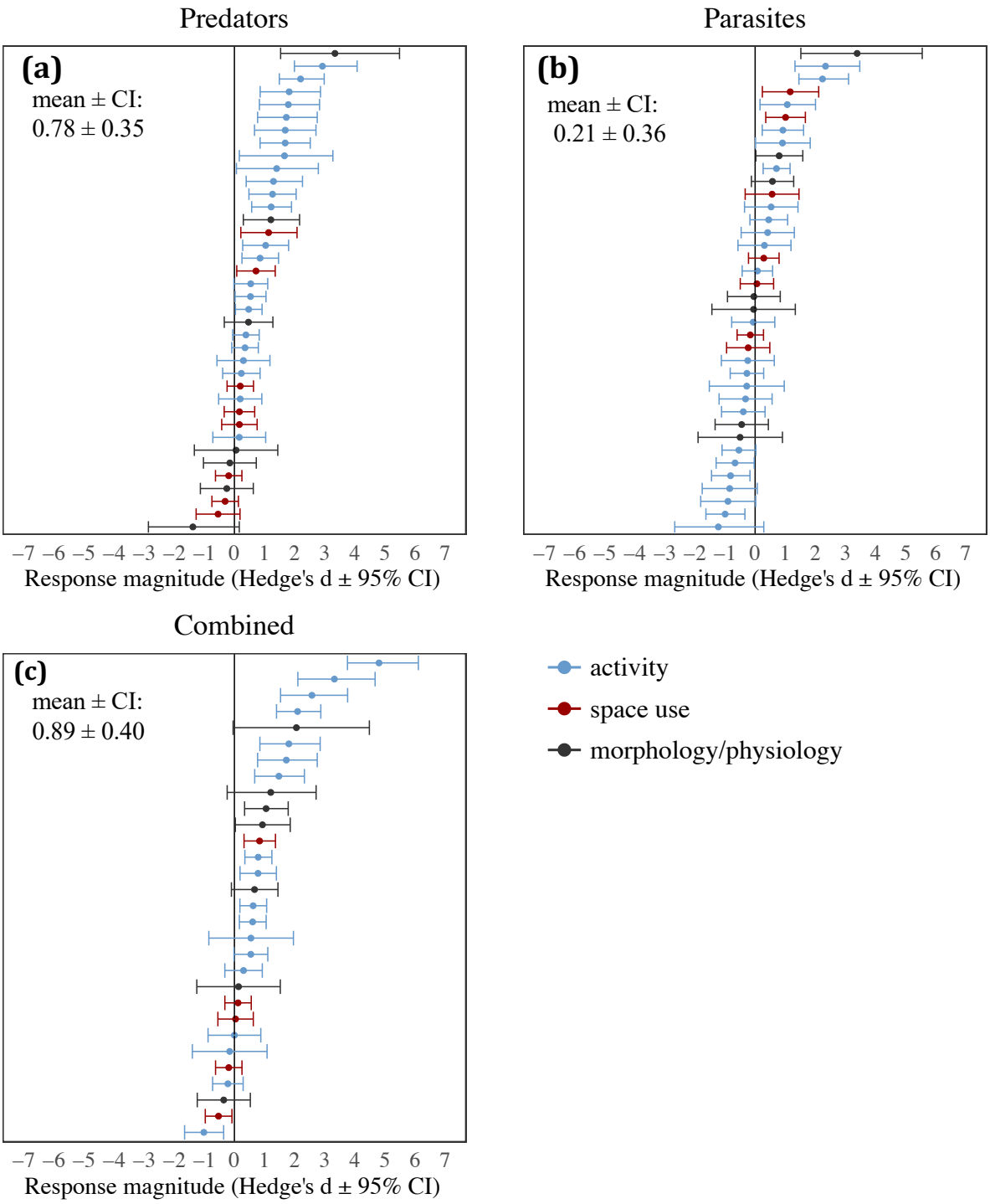
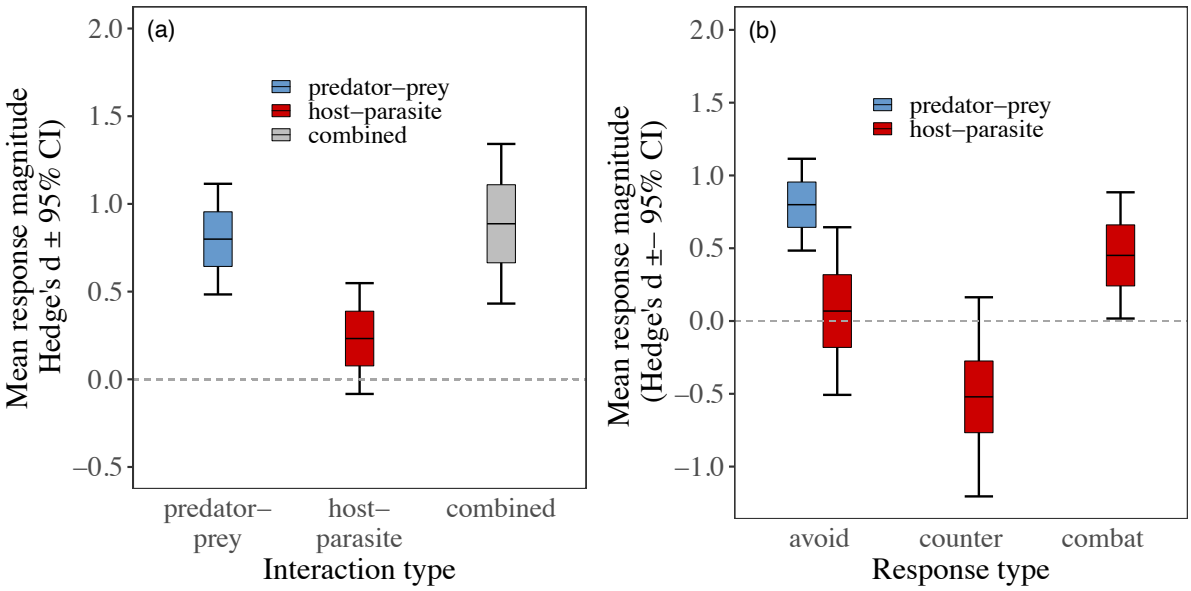

Predators
(a)
mean ± CI:
0.78 ± 0.35
−7 −6 −5 −4 −3 −2 −1 0 1 2 3 4 5 6 7
Response magnitude (Hedge's d ± 95% CI)
Parasites
(b)
mean ± CI:
0.21 ± 0.36
−7 −6 −5 −4 −3 −2 −1 0 1 2 3 4 5 6 7
Response magnitude (Hedge's d ± 95% CI)
Combined
(c)
mean ± CI:
0.89 ± 0.40
−7 −6 −5 −4 −3 −2 −1 0 1 2 3 4 5 6 7
Response magnitude (Hedge's d ± 95% CI)
activity
space use
morphology/physiology

Fig. 3


(a)
predator–prey
host–parasite
combined
Mean response magnitude
Hedge's d ± 95% CI)
2.0
1.5
1.0
0.5
0.0
–0.5
predator–
prey
host–
parasite
combined
Interaction type
(b)
predator–prey
host–parasite
Mean response magnitude
(Hedge's d ±– 95% CI)
2.0
1.5
1.0
0.5
0.0
–0.5
–1.0
avoid
counter
combat
Response type