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Linking anti-predator behaviour, ingestion, gut evacuation and costs of predator-induced responses in tadpoles

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Many prey organisms reduce their activity to reduce predation risk. A common argument is that a reduction in activity is one of the highest costs of defence. Here, I report an experiment that exposes predator-induced and predator-naïve morphs to a short-term predator environment and record behavioural, life-historical, physiological, and morphological responses. In contrast to expectation, reduced activity is not one of the highest costs of responding to predators. Predator-exposed tadpoles ingested the same amount of food with less feeding effort and evacuated food from their guts at a higher rate. Despite these advantages, predator-exposed tadpoles still paid costs in responding to predators, in decreased development rate. They did not have reduced survival or reduced growth. Costs in responding to predators are likely caused by physiological factors, such as reduced conversion rates, increased metabolic rates or by allocation to morphological defences, such as increased tail depth. My results show that feeding activity is not linked to the amount of food ingested and that physiological mechanisms -such as gut evacuation- decouple feeding activity and ingestion from growth, development and survival. There was no adaptive response in gut morphology. My study improves the understanding of the underlying internal and physiological mechanisms mediating the trade-off between activity and costs of predator-induced defences.

Key-words: Anura, assimilation, feeding activity, growth/predation risk trade-off, phenotypic plasticity, *Rana lessonae*, physiological plasticity, digestion efficiency.

Many prey organisms express defences under predation risk (Lima, 1998). One predator-induced defence is reduced activity, which proved to be one of the most efficient behavioural defences in several previous studies, in which reduced activity resulted in reduced encounter rates with predators, decreased detection by predators, and increased time spent hiding and seeking shelter (Werner & Anholt, 1993; Lefcort, 1996; Stoks et al., 2003; Stoks et al., 2005). However, defences do not come without costs (Via & Lande, 1985). Reduced activity should lead to less time spent feeding and less time searching for food, which should result in a reduced amount of food ingested, and this, in turn, should result in reduced growth, development and reproduction (Belovsky, 1978; Werner & Anholt, 1993).

The argument that reduced activity is one of the highest costs of defence has been widely used in empirical and theoretical studies (Werner & Anholt, 1993; Mcnamara & Houston, 1994; Lima, 1998; Van Buskirk, 2000; Relyea, 2001; Yearsley et al., 2002; Benard, 2004; Hoverman et al., 2005; Noonburg & Nisbet, 2005; Steiner & Pfeiffer, 2007), though evidence for this basic assumption is lacking in many predator-prey systems (Lima & Dill, 1990; McPeck et al., 2001; McPeck, 2004), and the mechanistic link between reduced activity and cost of defence lacks widespread empirical support (McPeck et al., 2001; McPeck, 2004; Relyea & Auld, 2004). Recently, it has been shown that the link between activity level and corresponding growth and development rates is not as clear as previously assumed (Anholt et al., 2000; McPeck, 2004). We need a better understanding of the mechanisms mediating the trade-off between activity and costs of predator-induced defences to be able to link reduced activity to cost of defence.

To disentangle linking mechanisms, we can take advantage of differences in time lags in plastic responses to environmental changes. Behavioural mechanisms should respond quickly, morphological responses should have a substantial time lag, and physiological responses could either be fast or require some time to adjust. Experimental comparison of the exposure of predator-naïve and predator-induced morphs to caged predators allows the

evaluation of time lags and provides insights to mechanisms that mediate costs. For example, both predator-naïve and predator-induced morphs might show reduced feeding activity when exposed to predation risk and a concomitant reduced amount of food ingested, but only induced morphs show increased digestion efficiencies (high proportion of ingested food assimilated); we would conclude that feeding and ingestion adjust quickly to environmental changes, whereas digestion physiology has substantial time lag and is not mechanistically linked to feeding activity and ingestion.

Here, I evaluate whether decreased feeding activity under predation risk is one of the major costs of responding to predators. I investigated plastic responses in activity, ingestion, gut evacuation, and gut morphology of predator-induced and predator-naïve tadpoles. I also examined the relationship of such responses to survival, development and growth. To disentangle internal mechanisms I exposed predator-induced and predator-naïve morphs to environments without and with caged predators. A system well-suited to address these questions is the predator-prey system with tadpoles as prey organisms and dragonfly larvae as predators, a well-established system for studying costs of predator-induced responses. Predator-exposed tadpoles show reduced swimming and feeding activity and increased hiding. Cost of responses are often expressed in reduced survival, reduced development, and reduced growth (Werner & Anholt, 1993; Relyea & Werner, 1999; Eklöv & Halvarsson, 2000; Van Buskirk, 2000; Peacor & Werner, 2001; Richardson, 2001; Van Buskirk, 2002a). I expected that predator-exposed tadpoles would reduce their feeding activity, decrease their food intake and show higher digestion efficiencies, because reduced food intake would lead to high digestion efficiency (Steinwascher, 1979; Horiuchi & Koshida, 1989). I expected morphological responses only between predator-induced and predator-naïve morphs. Induced morphs should have increased morphological defence, i.e. deeper tail fins, gut morphology that increase digestion efficiency, that is longer and thinner guts, and reduced growth and development rates. I did not expect morphological responses to short-term exposure to

different predator environments, because morphological adaptations should not respond within only a few hours.

METHODS

Experimental Design

For the experiment I used tadpoles of the pool frog *Rana lessonae*. Their responses to predators are well known (Van Buskirk, 2002a). First, I reared tadpoles in outdoor pools with and without caged predators to induce a predator-adapted morph (hereafter induced morph) and a predator-naïve morph (hereafter naïve morph). In a second step, I exposed both morphs to predator and no-predator environments during a short-term feeding trial. This resulted in a two-by-two full factorial experimental design with two morphs and two short-term feeding trial environments where the experimental design unit consists of three tadpoles of one morph experiencing one of the two feeding trial environments. I conducted both parts of the experiment in 0.28-m² plastic pools filled with 80 litres of aged tap water, located in an outdoor field at the University of Zürich, Switzerland. I covered all pools with shade cloth lids to avoid colonization by predators. Tadpoles came from clutches of eggs produced by pairs of *R. lessonae* collected 22 km east of Zürich.

Induction of Predator-induced and Predator-naïve Morphs

I conducted the induction of the two morphs in 20 pools, randomly assigned to two predator treatments, half with and half without predators. The predator pools contained one floating cage (~1 L volume) with one final instar dragonfly larva (*A. cyanea*). The no-predator pools contained an empty floating cage. Throughout the experiment the caged dragonfly larvae were fed 300 mg of *R. lessonae* tadpoles three times a week and were rotated to equalize any possible difference among individual *Aeshna*. In no-predator pools I switched cages to control for the effects of disturbance. I stocked the pools with zooplankton and 3.1 g of a mixture of rabbit chow and fish food. I added supplements of 2 and 4 g of rabbit chow 18 and 22 days

after the start of the experiment. At the outset of the induction of the two morphs, I randomly assigned replicates of seven tadpoles each (25 tadpoles/m²) to the 20 pools. When I stocked the pools on 30 July 2002 the tadpoles were at Gosner (1960) stage 28–29 and weighed on average 82 mg. The induction of morphs lasted for 24 days. During the induction some tadpoles died. At the end of the induction, I replenished tadpoles from one of the original ten pools with the same predator treatment to the remaining nine pools. I did this to obtain nine pools each containing six tadpoles with the induced morph and nine pools each containing six tadpoles with the naïve morph for the feeding trial.

Feeding Trial

I conducted a 4 hour feeding trial on 22 August 2002, one day after I fed the dragonflies. The goal was to measure ingestion and gut evacuation between the induced and naïve morph in response to two environments (with caged predator and no-predator) by inducing two visible marks at 2 hour intervals in the gut.

I induced the marks by placing the six tadpoles from each pool for 5 minutes in a box containing one litre of a 300 mg/l solution of fluorescent dye composed of 122 mg of fluorescent particles (Magruder Color Company JST–300 Series) and 178 mg of ground rabbit chow. The tadpoles ingested the mixture of colour particles and food by normal feeding which resulted in a distinctive colour mark in the gut (Eklöv & Halvarsson, 2000). Under normal feeding the mark moves from the oesophagus through the gut and is defecated 6-7 hours after the induction. The feeding behaviour and the time the food abided in the gut did not differ for individuals with or without marks when exposure to colour particles was only for a short time. The use of colour particles enabled me to use different colour marks to distinguish between morphs.

At the outset of the feeding trial and after inducing the first mark in the gut I divided the six tadpoles from each pool in two release groups: three were released into a pool with a caged predator and three into a pool with no-predator. Thus the group of three shared the same

induction history (morph) and the same feeding trial environment. Therefore, after I set the first mark, each of the 18 pools had six tadpoles, three tadpoles with the induced morph and three with the naïve morph, and half of the pools had predators, half no-predators. My experimental design assured that the two groups with different induction histories that shared a pool for the feeding trial were exposed to the same resource levels during the feeding trial. It is known that prey behaviour in response to predation risk can alter resource levels in unexpected ways (Peacor, 2002). After 2 hours of normal feeding, I induced a second mark in the gut and released the tadpoles again into the same pool (Fig. 1). Another 2 hours later, 4 hours after the start of the feeding trial, I sacrificed the tadpoles by an overdose of the anaesthetic benzocaine and preserved them in 10% formalin for further analysis.

Measurements, Calculations and Analyses

At the end of the induction period and before replenishing tadpoles, I assessed survival in each pool. Two days before the feeding trial, I recorded behaviour data via the instantaneous sampling of the activity of the visible tadpoles as swimming, feeding or resting (Horat & Semlitsch, 1994). I recorded the behaviour data by visiting each pool six times over a 6 hour period on August 20, one day after I fed the dragonflies. After performing the feeding trial on August 22, I weighed the preserved tadpoles, ascertained their developmental stage (Gosner, 1960), photographed them in lateral and ventral view, and estimated body size as the centroid size calculated from 26 landmarks positioned in three-dimensional space using imaging analysis software (Optimas 6.5, Media Cybernetics 1999) (Bookstein, 1991; Steiner, in press). I also used the photographs to measure tail depth, a morphological defence trait (Van Buskirk, 2000). After I collected these external morphometric traits, I dissected the tadpoles and measured the gut width, gut length and the distance from the oesophagus to the first and second mark (Fig. 1). With these measurements I calculated the volumes of the three different parts of the gut, assuming circular transverse sections of the gut (Fig. 1).

I defined ingestion as the gut volume between the oesophagus and the second mark, i.e. the amount of food ingested within the final 2 hours which was not already evacuated (removed from the gut, assimilated from the gut) within these 2 hours (Fig. 1). I defined gut evacuation by calculating the proportion between the amount of undigested food that had been ingested within the final 2 hours divided by the amount of undigested (not assimilated or evacuated) food that had been ingested within the last 4 hours (Fig. 1). Note that gut evacuation was not measured as defecation. For these calculations, I had to assume a constant feeding rate over the 4 hours of the feeding trial and a direct correlation between volume and amount of food in all parts of the guts. By using intervals of 2 hours, the ingestion and evacuation data related directly to ingestion and evacuation rates, and should be correlated to the assimilation rate. For example, without any evacuation of food the ratio is expected to be 0.5, with increasing evacuation the ratio between the volume 1 over volume 1 and 2 increases (Fig.1).

Two of the 108 individuals were excluded from the analysis, because one or both marks had already been excreted. I could not determine development stage of tadpoles for one pool due to technical problems. I analysed the effect of predator exposure during the morph-induction on survival and feeding activity with ANOVA. I corrected tail depth and gut morphology measurements for body size by taking the residuals of each trait after regression against body size and body size squared. Using these residuals I did a repeated measures ANOVA (SAS 8.02 proc glm; type III SS; SAS Institute 1998) with the feeding trial environments as within-subject effect and the two morphs as between-subject effect. I did the same repeated measures ANOVA with development stage, body size, body mass and gut evacuation as response variable. The unit of observation was the mean of three tadpoles that were reared in the same morph-induction pool and experienced the same environment in the feeding trial.

RESULTS

As expected, the tadpoles reduced their feeding activity in response to predator exposure from 15.5% (± 2.0 SE) to 6.7% (± 2.2 SE) ($F_{1,18}=8.795$, $p=0.008$), reduced swimming activity and increased time spent resting. Fast behavioural responses of tadpoles to changing predation risk have been demonstrated previously (Eklöv & Halvarsson, 2000; Van Buskirk, 2002b). In contrast to expectations, there was no response in the amount of food ingested during the final 2 hours of the feeding trial (Fig.2a, Table 1). The decrease in feeding activity did not lead to a decrease in food ingestion. Induced morphs tended to ingest 19.1 % more food than naïve morphs (Fig. 2a, Table 1), which is an indicator that ingestion might be linked to the morph, i.e. long-term induction and not short-term exposure to predators.

Gut evacuation responded only to feeding environment, with tadpoles in the predator environment evacuating 11.8% more food than tadpoles in the no-predator environment (Fig. 2b, Table 1). Therefore, gut evacuation is not linked to the morph, but the underlying physiology to evacuate food from the gut adapts quickly to changes in the environment, such as presence of predators. This fast physiological response indicates that disturbances during the feeding trial to induce the gut mark did not stress the tadpoles to such a degree that any fast physiological response was masked.

In contrast to expectations, there was an interaction effect between morphs (induction) and feeding trial environment on gut morphology (gut length, gut width and gut volume). Naïve morphs had longer guts when exposed to predators in the feeding trial compared to naïve morphs in the no-predator environment, whereas induced morphs showed the opposite pattern (Fig. 2c, Table 1). Gut width showed only a response to the feeding trial environment, with predator-exposed tadpoles having 4.6% wider guts than tadpoles in the no-predator environment (Fig. 2d, Table 1). Total gut volume was mainly influenced by the difference in response of naïve morphs to the two feeding trial environments (interaction between morph and feeding trial, Fig. 2e, Table 1). Naïve morphs held 20.5% more volume in their guts when

exposed to predators than when not exposed to predators during the feeding trial. Induced morphs showed a 6.8% response in the opposite direction. These unexpected responses in gut morphology are hard to interpret, but gut morphology might be largely affected by the amount of food in the gut, because tadpole guts, especially of herbivorous tadpoles, are very thin with little muscle and very flexible (Horiuchi & Koshida, 1989).

The other morphological and life-history traits -tail depth, development, and body size- responded as expected mainly to the long-term induction. Induced morphs increased their tail depth by about 7% (Fig. 2f), a morphological defence mechanism which reduces predation (Table 1)(McCollum & VanBuskirk, 1996). Costs for responding to predators were only paid by reduced development in induced morphs (Fig. 2g, Table 1). There were no costs for responding to predators through survival ($F_{1,18}=0.022$, $p=0.883$), or body size (growth)(Table 1, Fig. 2h). I used body size rather than body mass to estimate growth, because the total body mass is 50% gut content and therefore correlates with the amount of food in the gut (Calef, 1973).

DISCUSSION

High feeding activity does not result in high amounts of ingested food -food which was ingested but not already evacuated from the guts within the final two hours- and the common assumption that decreased feeding activity under predation risk is one of the major costs of responding to predators is misleading. Predator-exposed tadpoles ingested the same amount of food with less feeding effort and evacuated food at a higher rate, which should lead to the unusual expectation that predator-exposed tadpoles should show faster development, higher growth, and higher survival (Peacor, 2002). Despite the ability of predator-exposed tadpoles to reduce the impact of avoiding predators by ingesting the same amount of food with less feeding effort and evacuating food at a higher rate, they still pay costs in responding to predators by a decreased development rate. Decreased feeding activity under predation risk is

not a major cost of responding to predators. Other costs, such as increased investment in tail depth or physiological mechanisms might be responsible for reduced development.

Feeding activity is not linked to the amount of food ingested, which supports studies on insect larvae, where more active damselfly larvae did not ingest more food (McPeck, 2004). My results also support studies that show that physiological responses, such as digestion or gut evacuation can decouple growth from behaviour responses (McPeck, 2004; Stoks et al., 2005). The fact that predator-exposed tadpoles ingest similar amounts of food and evacuate food at a higher rate but do not show increased growth rates, survival or development, might indicate that exposed tadpoles convert evacuated food at a lower rate into body mass, i.e. they show lower growth efficiency, similar to damselfly larvae (Stoks et al., 2005). Another study on damselfly larvae showed that despite no difference in ingestion or assimilation rate, more active species were able to convert food more efficiently into body mass in a predator environments (McPeck, 2004). This implies that physiological mechanisms other than assimilation and gut evacuation affect the conversion of ingested food into body mass under predation risk. Increased metabolic rate might be one of these mechanisms. Increased metabolic rates have been suggested as a response to predator exposure in other species (Rovero et al., 1999; Stoks, 2001; McPeck, 2004), with ambiguous evidence in tadpoles (Steiner unpublished). High metabolic rates might allow high evacuation rates but might be more a side effect of an increase in the response rate to striking dragonflies and an increase in burst speed, which reduces predation (Fitzpatrick et al., 2003). Unfortunately, I have not measured conversion rates or metabolic rates in this experiment.

Response to predation resulted in reduced developmental rates, but not in reduced survival or reduced growth. The lack of growth or survival costs have been found in a number of other studies on tadpoles (Skelly, 1992; Laurila et al., 1998; Van Buskirk, 2000; Babbitt, 2001). Costs of response can be explained by either costly physiological responses such as increased metabolic rates, or by costs of morphological defence traits such as increased tail

depth. Such costs of responding to predators must outweigh positive effects on evacuation rates and feeding efficiency of predator-exposed tadpoles, because optimal foraging theory, theory about the evolution of phenotypic plasticity and life-history theory suggest that tadpoles in non-predator environments would develop the same morph, behaviour, life-history or physiology if there were no extra costs involved (Seale & Beckvar, 1980; Pyke, 1984; Via & Lande, 1985; Stearns, 1992).

There is no adaptive response in gut morphology. The gut did not respond to 24 days of exposure to predators; all observed differences in gut morphology are likely affected by the proximal filling of the gut. Despite a tendency for longer guts in the naïve morph, my results do not support the only other study which assessed effects of (long-term) predator exposure on gut length where predator-exposed tadpoles had shorter guts (Relyea & Auld, 2004). Relyea and Auld (2004) argued that longer guts allowed food to digest more efficiently and explained higher growth rates of naïve tadpoles. This argument is not supported by my results. Fast responses in evacuation rates did not relate to gut length, or any other gut morphology measure. Unfortunately, I did not measure the morphology of empty guts, which should allow measuring gut morphology independently of gut filling, though it is difficult to measure the thin and flexible empty guts without large measurement errors.

Simple models based on the idea that feeding activity and ingestion are maximised and positively linked (Belovsky, 1978; Werner & Anholt, 1993; Werner & Anholt, 1996; Abrams, 2003) are not sufficient to explain the observed pattern. However, models based on optimal food intake that maximise growth and fitness by balancing the benefits and costs of ingestion are supported by my results (Yearsley et al., 2002). In these models the costs of food intake are divided into extrinsic costs associated with the activity of feeding, intrinsic costs of food intake itself, and costs associated with digestion (Yearsley et al., 2002).

My experiment showed that there is a complex interplay between behaviour, life-history, morphology and physiology. Feeding activity is decoupled from ingestion and the

link of both traits to growth is more complex than previously assumed and mediated by various physiological mechanisms. Ingestion and gut evacuation are not functionally linked mechanisms and act independent from each other. Ingestion did not respond to short-term predator exposure, whereas the evacuation rate adjusted quickly to environmental changes in exposure to predators. This interplay between behaviour, life-history, morphology, and physiology adds and counteracts induced costs in different environments. It shows that the role of physiology, often ignored or underestimated by ecologists, can alter the interpretation of experiments and add to the complexity of interactions in the costs of induced defences or more generally of plastic responses. Physiological plastic responses can alter cost-benefit ratios of defence mechanisms and thereby change predator-prey interactions, and community and population dynamics. Very likely other shifts in physiology as response to predation risk await future discovery and description. Promising approaches to investigate specificity and sensitivity of such physiological responses to predation risk, have been laid out by studies exploring various behavioural, life-historical and morphological responses to different predators and different chemical cues (Lefcort, 1996; Laurila et al., 1997; Laurila et al., 1998; Van Buskirk, 2001; Van Buskirk & Arioli, 2002; Relyea, 2004; Kishida & Nishimura, 2005).

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Table 1: Repeated measures ANOVA on external and intestinal morphological traits and feeding traits with the two morphs (induced and naïve, long-term predator effect) as between subject effect and the short-term feeding trial (predator and no-predator exposure) and the interaction between morph and feeding trial as within subject effects. All tests have 1,16 df, except the test for development stage (1,14 df). The tests for food ingested, gut length, gut width, gut volume, and tail depth were performed with body size corrected data. Bold values indicate significant results.

response	Morph F (p)	Feeding trial F (p)	Morph x Feeding trial F (p)
Food ingested	3.31 (0.087)	0.48 (0.499)	0.45 (0.514)
Gut evacuation rate	0.09 (0.773)	12.38 (0.003)	0.06 (0.812)
Gut length	2.83 (0.112)	0.48 (0.497)	13.86 (0.002)
Gut width	3.42 (0.083)	6.84 (0.019)	1.40 (0.254)
Total gut volume	0.42 (0.525)	2.69 (0.121)	4.74 (0.045)
Tail depth	13.25 (0.002)	0.48 (0.496)	0.61 (0.448)
Development stage	9.22 (0.009)	3.27 (0.092)	2.24 (0.156)
Body size (Centroid size)	0.69 (0.419)	0.17 (0.687)	0.78 (0.390)

Fig. 1: Gut width measurements were taken at the oesophagus, in the gut middle and at the anus. Distances between the oesophagus, the anus, and the first and second marks were taken. These measurements were used to calculate the volumes for three gut areas 1. oesophagus to second mark (volume final 2 hours), 2. second to first mark (volume 2 to 4 hours) and 3. first mark to anus (remaining volume) respectively. Ingestion is defined by volume 1., and gut evacuation by volume 1./(1.+2.).

Fig. 2: Ingestion (a), gut evacuation (b), gut length (c), gut width (d), total gut volume (e), tail depth (f), development stage (g), and body size (h) responses of predator-induced and predator-naïve morphs of *Rana lessonae* tadpoles in a short-term feeding trial with a predator and no-predator environment. Symbols show means \pm 1 SE of nine replicates (development eight replicates) in the feeding trial with filled symbols for the naïve-morphs and open symbols for the induced morphs. Units for development are given in Gosner (1960) stage.

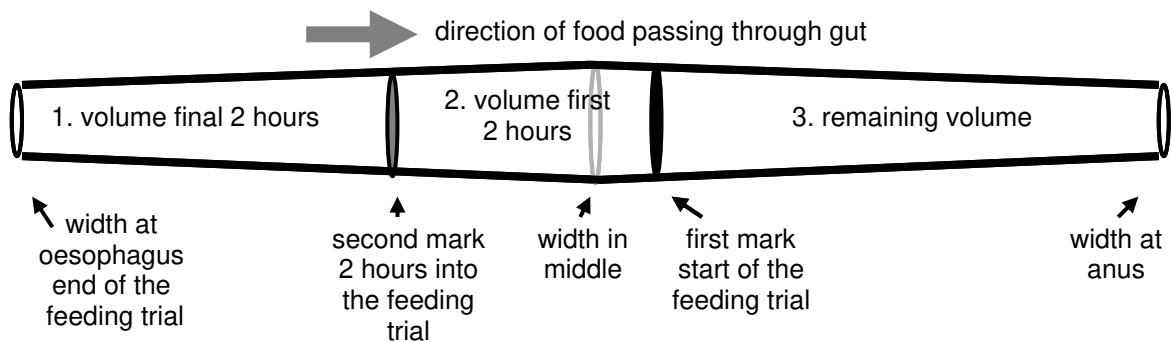


Fig. 1

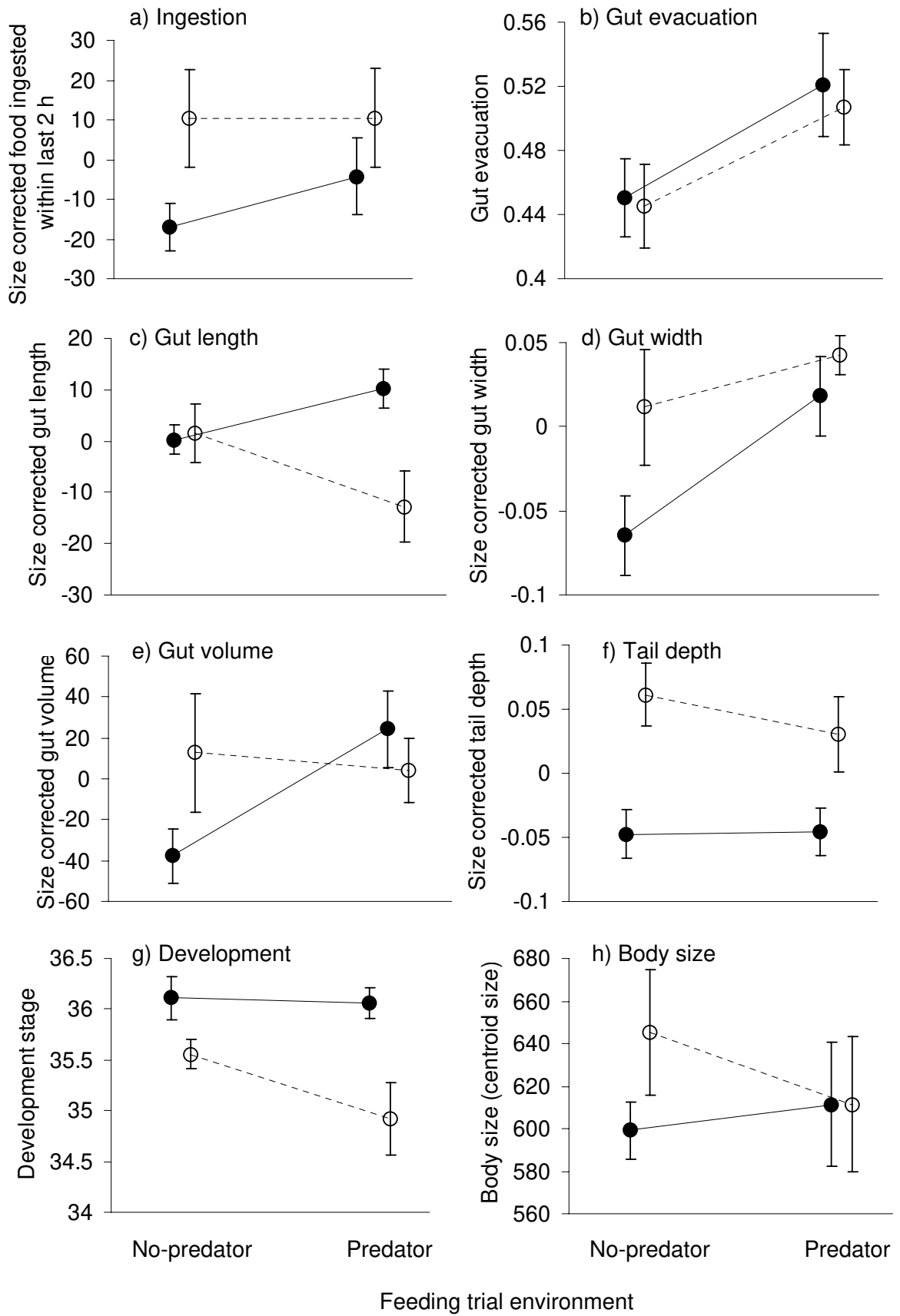


Fig. 2