The prey perspective - behaviour and appearance in a world of predators

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Behaviour and appearance in a world of predators

Johan Ahlgren

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Abstract

The varieties of prey phenotypes that have been revealed in nature are vast and many of these phenotypes are the result of the selective force that predators have had on prey traits in the past. Even within species and populations we see variations due to both differences in the selection forces they live under but also due to individual trait variation. In this thesis I investigate both the direct and indirect effects that predators have on two freshwater prey species, focusing especially on prey defence traits. In addition, the unexplained variation around average trait values in my and other studies led me to also study the effects of animal personalities on anti-predator adaptations.

I found evidence for indirect effects on the adaptations to the dominant predator regime in *Gammarus pulex*. Individuals adapted to a life in the presence of predatory fish spent more time in refuges and had a higher non-consumptive mortality. Males seem to be the most affected sex as they had higher mortality than females, but also because they had to trade-off their mate-guarding behaviour due to an increased risk of fish predation. The freshwater snail *Radix balthica* showed plasticity in their mantle pigmentation when exposed to both predatory fish and ultraviolet radiation (UVR). In the presence of fish they got more complex pigment patterns. When exposed to UVR and UVR combined with fish, snails responded with increasing their pigmentation even further, which led to a loss in pattern complexity, suggesting a trade-off between photoprotection and camouflage. These snails also showed a trade-off when exposed to fish and leech predators simultaneously. The presence of leeches in refuges force snails out in the open, facilitating fish predation. Since these indirect effects of leeches are only present when leeches are combined with fish, they have earlier been overlooked as a fish effect.

When zooming in on individual snails, they showed consistence in a personality trait associated with risk taking (boldness). This means that some snails are shy and others are bold across contexts. In fish-free ponds, dominated by invertebrate predators like leeches, I could not find any selection for either bold or shy snails. On the other hand I found, both in the lab and in the field, that in fish ponds, bold snails survived to a greater extent than shy snails. One explanation for this is that bold snails also had a shell with a rounder shape and bigger aperture, providing better protection from shell crushing predators like fish.

My work reveals some new insights in how predators have shaped prey phenotypes through years of selective predation. In addition to the non-consumptive effects that predators have on prey phenotypes its clear that phenotypes that are badly adapted will quickly be removed from the population. Intriguingly, I also found that predators can shape the distribution of animal personalities and give rise to phenotypic compensation, where bold individuals compensate their risky life style with more pronounced defence traits.

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Local adaptation, predator regime, phenotypic plasticity, inducible defence, mortality, animal personality, predator, trait-compensation

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SAMMANFATTNING PÅ SVENSKA

Den enorma variationen av beteenden och utseenden som återfinns i djurriket har i alla år fascinerat och länge förbryllat biologer. Rovdjurens skoningslösa utgallring är en av de stora drivkrafterna bakom evolutionen av alla dessa karaktärsdrag. Rovdjuren är såklart även en viktig strukturerande kraft i sötvattensmiljöer och har där lett till utvecklingen av mängder av försvarsanpassningar hos bytesdjuren, inklusive beteendeförändringar, kroppsliga- och kemiska-försvar. Även om vi vet mycket om hur rovdjur påverkar bytesdjurens beteenden och utseende så finns det fortfarande otaligt med obesvarade frågor. I min avhandling försöker jag svara på några av de frågor som berör den stora variationen vi ser inom arter, ja, till och med inom samma bestånd.

Jag har studerat två olika vattenlevande bytesdjur, sötvattensmärlan och den ovala dammsnäckan. Snäckan är väldigt flexibel och kan till exempel känna igen och ändra beteende och skalform vid doften av rovfisk, oavsett om den tidigare levt med eller utan fisk i sin närvaro. Sötvattensmärlan är däremot känd för att vara lokalt anpassad och har till skillnad från snäckan även visat sig vara naiv i mötet med tidigare okända rovdjur. Sötvattensmärlor från fisk- respektive fiskfria-dammar skiljer sig därför åt i beteende, parningsstrategier och dödlighet till följd av deras lokala anpassningar till den rådande rovdjurssammansättningen. Den höga dödlighet som jag såg hos individer från fiskdammar jämfört med de från fiskfria-dammar kan bero på att det blir ökad konkurrens och mer aggression mellan individerna när sötvattensmärlorna tvingas spendera mer tid i gömsle för att undkomma rovfisk. Dessutom har sötvattensmärlshanar visat sig vakta honorna innan parning genom att helt enkelt klamra sig fast på deras rygg. I fiskdammarna såg jag att hanarna vaktade honorna i mindre utsträckning än i fiskfria dammar. Vidare kunde jag visa att det är klara skillnader mellan hanar och honor när det kommer till dödlighet och födointag, då hanar på grund av sin ”lev fort, dö ung-” livsstil hade både högre dödlighet och högre födointag än honor.

Snäckornas flexibilitet gör att de lämpar sig bra att använda till studier som försöker förklara hur flexibla försvar påverkar variationen av beteende och utseende hos bytesdjur. Hos sötvattenssnäckor med ljusgenomsläppligt skal har flera studier visat på skillnader i mängden samt mönstringen av deras kroppspigmentering. Enligt litteraturen är dessa skillnader en följd av artspecifika pigmenteringsmönster samt ärftliga skillnader mellan populationer inom arter. Vidare har man dock också sett stora variationer inom populationer, vilket tyder på polymorfism (förekomsten av två eller flera former inom en population). Därför undersökte jag om skillnaderna i mantelpigmentering kunde bero på skillnader i miljövariabler som rovdjursnärvaro och ultraviolett-strålning (UV). Det visade sig att individer från samma population kunde uttrycka ett stort omfång av både pigmenteringsmönster och mängden pigmentering. Snäckor som utsatts för rovfisk fick mer fläckig pigmentering, ett försvar som antagligen gör snäckorna mer kamouflerade. Snäckorna i UV-behandlingen blev ännu mörkare eftersom dessa melaninpigment har en skyddande effekt mot UV. En kraftig pigmentering omöjliggör samtidigt fläckig pigmentering och dessa snäckor var därför mindre kamouflerade än snäckorna i rovfiskbehandlingen. När jag sedan utsatte snäckorna för rovfisk och UV samtidigt, blev snäckorna lika mörka som i UV-behandlingen, men mindre fläckiga än de i rovfisk-behandlingen. Detta tyder på att snäckorna har svårt att optimera sin pigmentering när de utsätts för både rovfisk och UV. Med tanke på mängden mörka pigment hos snäckorna i UV-behandlingarna har de förslagsvis ett fullgott skydd mot UV. Däremot har snäckorna som utsatts för både rovfisk och UV fått prioritera bort sitt fläckiga kamouflage och har då antagligen ett sämre kamouflage än de snäckor som endast utsatts för rovfisk. Både rovfisk och UV framkallar mer pigment men med olika resultat, vilket gör det svårt för snäckorna att optimera sin pigmentering när de utsätts för rovfisk och UV samtidigt.

Vidare undersökte jag hur sötvattenssnäckan reagerade på närvaro av två rovdjur med olika jaktstrategier. Rovfisken rudan och snäckätande iglar använder olika jaktstrategier men har båda visat sig vara specialister på att fånga snäckor. Medan rudan aktivt letar efter snäckor, sitter igeln och väntar på att en snäcka ska krypa förbi. Fisknärvaro framkallade ett ökat utnyttjande av gömslen samtidigt som igelnärvaro minskade snäckornas användning av gömslen. Detta är ett tydligt exempel på när två rovdjursförsvar är i konflikt. När ett bytesdjur utsetts för flera rovdjur samtidigt finns det flera tänkbara utfall, så som att framkalla ett genomsnittligt försvar eller att ignorera ett av rovdjuren och enbart reagera på det som i stunden upplevs som farligast. När jag utsatte snäckorna för både fisk och igel ignorerade de fisken och lämnade gömslena i försvar mot igeln. Rovfiskar kan konsumera sötvattenssnäckor i mycket högre takt än iglar, ändå utgör iglar ett mer direkt hot än fiskar. Genom att driva snäckorna ut ur de fisksäkra gömslena, påverkade iglarna indirekt snäckornas överlevnad genom att öka risken för att de blir uppätna av en fisk. Så även om snäckorna i sig konsumerar relativt få snäckor kan de öka andelen som faller offer för rovfisk. På så vis kan tillsynes oviktiga rovdjur spela en avgörande roll och ha en minst lika stor strukturerande effekt på bytesdjurstätheter som fisk anses ha.

För att beskriva de variationer i försvarsanpassningar som uppvisas mellan individer som lever i samma miljö har man under senare år börjat studera bytesdjurens personligheter. Precis som människor så skiljer sig andra djur också åt i karaktärsdrag så som benägenhet att ta risker, aktivitetsnivå och nyfikenhet. När det gäller studier som berör samspelet mellan rovdjur och bytesdjur är karaktärsdrag relaterade till benägenheten att ta risker extra intressanta. Det finns klara fördelar med att vara mindre rädd, då man t.ex. kan hitta mer föda och fler partners. I närheten av rovdjur kan det dock vara direkt farligt att vara mindre rädd, eftersom man riskerar att även träffa fler rovdjur. Jag använde mig av ett mått av snäckors risktagande för att studera hur detta påverkar risken för att bli uppäten av fisk och igel. Det visade sig att där inte fanns någon skillnad i dödlighet mellan försiktiga och risktagande snäckor i närvaro av igel. Även om risktagande individer kan tänkas leva under större risk klarade de sig bättre än de försiktiga snäckorna när de utsattes för rovfisk. För att bekräfta om dessa försöksresultat

speglade naturliga förhållanden samlade jag in snäckor från fisk- och fiskfria-dammar för att sen kvantifiera deras personlighet. Det visade sig att snäckor från fiskdammar var mer benägna att ta risker än snäckor från fiskfria-dammar. Dessutom fanns det nästan enbart risktagande snäckor i fiskdammarna medan det i fiskfria-dammar fanns en större variation av personligheter med både risktagande och försiktiga individer. Detta visar tydligt på rovdjurens inverkan i uppkomsten och upprätthållandet av personligheter i djurriket. Vad är det då som gör att risktagande snäckor klarar sig bättre än försiktiga snäckor i fiskdammar? Vi vet sedan tidigare att snäckor använder ett rundare skal för att försvara sig mot rovfisk. Därför födde jag upp snäckor och letade efter samband mellan deras skalform och deras benägenhet för att ta risker. Mycket riktigt visade det sig att risktagande snäckor hade en mer skyddande skalform än vad försiktiga snäckor hade, vilket tyder på en parallell selektion av både risktagande och skalform från rovfisk i det förflutna.

Sammanfattningsvis visar mina resultat på ytterligare några exempel där rovdjur har spelat en avgörande roll i evolutionen av bytesdjurens beteende och utseende. Dessutom har jag hittat tydliga samband mellan personligheter och den variationen i beteende och utseende som bytesdjuren uppvisar.

LIST OF PAPERS

This thesis is based on the following papers, referred to by their roman numerals:

I. Ahlgren, J., Åbjörnsson, K. & Brönmark, C. (2011)
The influence of predator regime on the behaviour and mortality of a freshwater amphipod, *Gammarus pulex*.
Hydrobiologia 671: 39-49.

II. Ahlgren, J., Yang, X., Hansson, L.-A. & Brönmark, C. (2013)
Camouflaged or tanned: plasticity in freshwater snail pigmentation.
Biology Letters 9(5).

III. Ahlgren, J. & Brönmark, C. (2012)
Fleeing towards death leech-induced behavioural defences increase freshwater snail susceptibility to predatory fish.
Oikos 121(9): 1501-1506.

IV. Ahlgren, J., Kinnby, A., Chapman, B., Nilsson, P.A. & Brönmark, C.
Fish favour the bold: predator regimes drive survival and distribution of animal behavioural types.
Submitted.

V. Ahlgren, J., Chapman, B., Nilsson, P.A. & Brönmark, C.
Phenotypic compensation in bold snails: boldness linked with protective shells.
Submitted.

Introduction

Nature is full of spectacular behaviours and appearances, which have always puzzled and fascinated biologists. Since the days Alfred Russel Wallace travelled the Indonesian archipelago we know that all this variation result from the different environmental conditions and the selection pressure these have on animal traits (Wallace 1858). Among the biotic factors, predation stands out as an especially powerful selection pressure on animal traits (Abrams 2000, Farkas and Montejo-Kovacevich 2014). Furthermore, predators differs in their choice of habitat (Relyea 2001), hunting strategies (Wooster 1994) and densities (Griffen and Williamson 2008), leading to wide range of potential anti-predator defences (Edmunds 1974). Hence, to match the present predation risk, prey has evolved defensive strategies in e.g. behaviour (Werner et al. 1983, Dalesman et al. 2014), morphology (Tollrian 1990, Brönmark and Miner 1992) and life-history traits (Crowl and Covich 1990, Laurila et al. 1998). Additionally, since prey in natural situations often are exposed to more then one threat simultaneously, prey constantly have to adapt their defensive phenotypes in response to both multiple predators and abiotic threats like ultraviolet radiation. However, even though many studies have combined several biotic and abiotic threats they cannot fully explain the intriguing individual variation in trait expression found within species or even within populations (Bolnick et al. 2011). Lately, its been argued that this individual variation in defence traits can be coupled to so-called “animal personalities” (Chapman et al. 2011, Hulthén et al. 2014, Kuo et al. 2014), but there are still numerous question marks to how and why personalities affect prey phenotypes. So even though we have come a long way since the days of Wallace and Darwin, there is still a lot more to learn about what factors affect prey phenotypes. Hence, in my thesis I focus on how factors like predation regime, multiple stressors, personalities and trait-compensation affect prey, both in a short-term, behavioural as well as in along-term evolutionary perspective.

PREDATOR DEFENCE

As I argued above, a whole range of fascinating adaptations like camouflage (Schaefer and Stobbe 2006), escape behaviours (Van Buskirk and McCollum 2000) and protective structures (Gilbert 2011) that we see in nature are the product of selective predation. This has led to an extensive variety of behavioural responses in prey that encounter or sense a predator, including reduced activity (Åbjörnsson et al. 2000), increased refuge use (Holomuzki and Short 1988, Åbjörnsson et al. 2000), avoiding areas where predators dwell (Skelly and Werner 1990), stay away from areas with dead conspecifics (Choh et al. 2010) or escaping an actual encounter (Townsend and McCarthy 1980). Another strategy often used by prey is to change morphology in response to predation threat, e.g. by changing to a more cryptic appearance (Whiteley et al. 2011) or by inducing a morphological defence prey may increase their probability of surviving a predator encounter (e.g. McCollum and Van Buskirk 1996, Relyea 2001). Further, these responses can be predator specific and prey are sometimes able to induce different defences depending on the hunting strategy of the predator (Van Buskirk et al. 1997, Van Buskirk and Relyea 1998, Hoverman et al. 2005, Lakowitz et al. 2008). All these defence adaptations are aimed at lowering the over-all risk of predation, but they come into action at different stages of the so-called predation cycle (search, encounter, prey detection, attack, capture and ingestion; Lima and Dill 1990, Brönmark and Hansson 2005). Therefore, some of the defence traits, e.g. hiding behaviours and camouflage, have evolved to lower the risk of predator encounters (Åbjörnsson et al. 2004, Dimitrova and Merilaita 2012), whereas others, like escape behaviours (McCollum and Van Buskirk 1996), size refuge (Nilsson and Brönmark 2000) and being poisonous combined with alarm signals (or the mimicry of alarm signals, Brodie III 1993), increase the probability of survival once encountered by a predator.

Furthermore, we know from the literature that prey may use two different strategies when expressing their defence. Prey that use a fixed/constitutive defence strategy always display the same phenotype, while prey with a plastic defence strategy can change their phenotype through so-called adaptive phenotypic plasticity. The plastic strategy allows one prey genotype to express several phenotypes dependent on the context. General theory predicts that if prey experience spatial and/or temporal changes in predation risk it would be more favourable to be plastic (Via and Lande 1987), while a fixed strategy is predicted for prey that experience a stable predation risk environment. The prediction that fixed genotypes are superior in stable environments are based on the assumption that there are several constraints associated with phenotypic plasticity, i.e. cost and limits (Dewitt et al. 1998). However, these costs of plasticity have been notoriously difficult to demonstrate and costs for the fixed/constitutive strategy are actually found to the same extent (Van Buskirk and Steiner 2009). What we do know is that for adaptive phenotypic plasticity to be successful, organisms need reliable cues about the present and future predation risk (Tollrian and Harvell 1999). The accuracy of these cues is especially important when inducing more costly and permanent changes, e.g. morphological defences. In addition to visual cues, there are a variety of other cues (e.g. mechanical and chemical) that prey can use to detect predators. For prey experiencing reduced visual conditions or for prey with poorly developed eyes, chemical cues are of great importance (Brönmark and Hansson 2000). These chemical cues can, in addition to detecting predator presence, give the prey more detailed information about e.g. predator diet and hunger level (Brönmark and Hansson 2012). Additionally, and most importantly, since these cues diffuse through the water, prey can get this information without encountering the predator.

THE KEY PLAYERS AND THEIR KNOWN DEFENCES

In this thesis, I have focused on two freshwater prey species, (in **paper I**) the amphipod *Gammarus pulex* and (in **papers II, III, IV** and **V**) the snail *Radix balthica*. The amphipod could be categorized as having two different phenotypes based on the predator regime of their habitat of origin. For example, an individual *G. pulex* from a fish pond have a lower activity and respond with an increased refuge use when exposed to cues from predatory fish, while individuals from a fish-free pond are more active and, as they are naïve to the fish cue as a threat they do not respond behaviourally. These behavioural differences among populations are genetically fixed and stable over generations (Åbjörnsson et al. 2004) and thus this is a great model species for studying effects of fixed differences between predator regimes. At a first glance the other model species used, *R. balthica,* also seems to be locally adapted to the prevailing predator regime. However, these differences are only due to phenotypic plasticity and common garden experiments show that independent on their origin they respond to fish cue by changing life history strategies, behaviour and morphology (Brönmark et al. 2011, Brönmark et al. 2012). Hence, this species is great for studying plastic defences in response to fluctuating threats.

NON-CONSUMPTIVE EFFECTS

While the consumptive effects are the most obvious effect predators have on prey, the non-consumptive effects of predators on prey can be diffuse and harder to identify. For example, predator induced changes in prey traits may reduce prey fitness (e.g. decreased survival), regardless of predatory killing (Boonstra et al. 1998). Additionally, predator induced defences, such as reduced activity, shift in habitat use and reduced feeding, will also affect other organisms using the same habitats/food sources (Peacor and Werner 1997, Bernot and Turner 2001). Furthermore, non-consumptive effects can be just as large or even larger then the consumptive effects and thus they are of great interest to study (Abrams 1990, Anholt and Werner 1995). So in addition to the differences in consumptive effects between predator regimes, prey may be exposed to quite different non-consumptive effects dependent on the prevailing predator regimes of their habitat. The main predator regimes that *G. pulex* are exposed to are fish and fish-free systems, and fish presence has previously been found to greatly affect *G. pulex* refuge use and life history strategies leading to local adaptations in these traits (Åbjörnsson et al. 2004, Åbjörnsson et al. 2009). In **paper I,** I look at more non-consumptive effects of these predator regimes. Hence, as a continuation of previous studies, I wanted to investigate the non-consumptive effects on mortality, anti-predator behaviour, mate-guarding and foraging from both predatory fish and predatory invertebrates. Further, I wanted to see if there were any sex specific differences with regards to these non-consumptive effects.

I performed two common garden experiments with *G. pulex* from ponds with predatory fish and fish-free ponds, where invertebrates are the dominating predators. In the first experiment I studied how predator regime (origin), predatory cues (from both fish and invertebrate predators) and sex affected refuge use, mortality and foraging rate in *G. pulex*. Male *G. pulex* commonly guard preferred females by grabbing hold of them until they are ready to mate and this pair-formation secures male mating opportunities. However, pair-formation comes with the cost of an increased risk of predation from fish, and, hence, I tested if there were any differences in pair-formation between *G. pulex* from fish and fish-free ponds and if there were any effects of predator presence (either fish or invertebrate predators) on this behaviour. Unlike earlier studies, there were no effects of predator cues on anti-predator behaviours probably due to that I measured behaviours after a longer time period (20 as opposed to 10 minutes in Åbjörnsson et al. 2004). This means that *G. pulex* already after 20 minutes have returned to standard behaviours, probably to minimise potential costs associated with their anti-predator behaviour (Anholt and Werner 1998). However, I found that that pond origin, i.e. predator regime, had a large impact on *G. pulex* refuge use, mortality and pair formation, even in the absence of predator cues. Individuals from fish ponds had a higher mortality and refuge use, but spent less time in pair-formation than individuals from fish-free ponds. The increased mortality in individuals from fish ponds could by explained by that they spent more time aggregated in the refuge, which potentially led to more interactions and hence more injuries and cannibalism (Plaistow et al. 2003). However, even if individuals from fish ponds showed increased refuge use and mortality their leaf-shredding rate, a main ecosystem service, was unaffected. Thus, as *G. pulex* uses their main food, leaf litter, also as a refuge they can continue to forage at the same rate as their conspecifics from fish-free ponds. When looking at male and female separately I found that there was no difference in refuge use, but that male individuals suffered higher mortality rates than females. One potential explanation is the aggressive nature of males linked to their mate searching (Krupa and Sih 1998) and mate-guarding behaviour (Dunn et al. 2008). I also found that males shredded more leafs then females, probably due to males being larger and having a "life fast, die young" life style (Bonduriansky et al. 2008) with higher metabolic rates (Fox et al. 2003) and, hence, a higher resource demand.

MULTIPLE STRESSORS

Ultraviolet radiation and predators

Even though prey defence traits are a well-studied phenomenon, it is only recently that the effect of an additional stressor on the expression of defence traits has been investigated. In nature, freshwater prey are of course not only exposed to a variety of predators, but also to abiotic stressors like temperature, wave action, drought and ultraviolet radiation (UVR). This gives the prey a great challenge, since a defence trait that may lower the risk of one threat may be useless or even maladaptive, increasing predation risk or susceptibility to other abiotic stressors (McIntosh and Peckarsky 1999, Laurila 2000, Gunzburger and Travis 2005, Hansson et al. 2007, Petrin et al. 2010). Hence, when a prey is exposed to more then one threat it has to trade-off its defence responses or, alternatively, only respond to the most relevant threat. The trade-offs between defences against predators and an abiotic stress such as UVR can be critical as UVR significantly harm organisms by affecting their behaviour, growth and damage their DNA (Caldwell et al. 1998, Belden et al. 2000). However, several organisms have the ability to induce photoprotective pigmentation that can counteract the harmful effects of UVR (Hansson et al. 2007, Hansson and Hylander 2009, Williamson et al. 2011). Another strategy is to behaviourally avoid contexts with high risk UVR as has been shown in, for example, Daphnia that avoid surface waters during daytime (Rhode et al. 2001). Regardless of the efficiency of the specific defences, when a prey is exposed to UVR and predation simultaneously they might run into trouble. Copepods have for example been found to ignore UVR when in environments where they are exposed to predatory fish and UVR simultaneously, hence to reduce predation risk they lose all their pigmentation making them more vulnerable to UVR (Hansson and Hylander 2009).

The freshwater snail *R. balthica* is a great model species for further studying potential trade-offs between defence adaptations against UVR and predation since they are known to vary greatly in their pigmentation (Falniowski 1980, Schniebs et al. 2011), but also because these air breading snails often dwell in shallow waters and crawls to the surface for air and predator avoidance, i.e. a microhabitat where they are highly exposed to UVR. Hence, in **paper II** I aimed to assess if this variations in mantle pigmentation are genetically fixed or if they are the effect of a defensive response to two common stressors, fish predators and UVR. I used a common garden experiment to test both the separate and combined effects of UVR and fish predators on the snail mantle pigmentation. This experiment had a 2x2 factorial design with four treatments; Control, Fish cue, UVR and Fish cue combined with UVR. When one week old, experiments started and snails were then exposed for eight weeks before I quantified their mantle pigmentation. I quantified two variables of pigmentation; first the amount of pigmentation as the ratio of dark vs. light pigmented area, and, secondly, as a measure of camouflage I used the complexity of the dark pigmented patches. I found that *R. balthica* is phenotypically plastic in both the amount and complexity of their mantle pigmentation. When exposed to fish, snails increased the amount of dark pigmentation, but without affecting the complexity of their pigmented patterns. This means that in comparison with snails in control treatment, these snails got a larger part of their mantle covered in complex patterns. I suggest that this is a disruptive coloration strategy to increase camouflage, where the patterns break the outline of the snail body (Fig. 1). The snails that were exposed to UVR increased the amount of

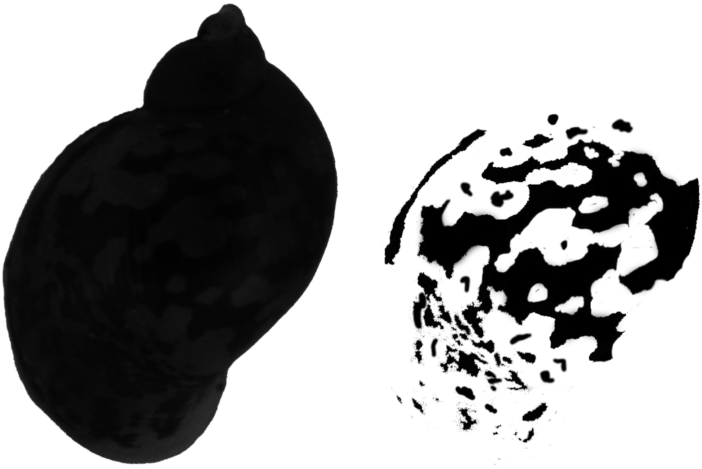

Fig. 1. The idea behind disruptive coloration is to break the outline of the body, consequently making it harder for predators to notice the prey. Here from the left, pictures with increased contrast to show the difference between a *Radix balthica* exposed to either ultraviolet radiation or fish respectively.

dark pigmentations even more, it actually increased so much that the possibility for a complex pattern decreased (Fig. 1 in **paper II**). The combination of fish and UVR induced the same amount of dark pigmentation as in the UVR only treatment, hence they also lost their pattern complexity. This means that the snails sacrifices their pattern complexity, and hence trade-off their camouflage for photoprotection. However, its still unclear if this trade-off constitutes a potential cost for snails in natural habitats, since snails may compensate their reduced camouflage by using e.g. anti-predator behaviour to a higher extent. An obvious potential benefit is that these photoprotected snails can use high UVR areas such as very shallow waters as well as staying close to the surface, where fish predation rates should be reduced.

Multiple predators

Predators may differ in their hunting strategies as well as in their choice of habitat, therefore prey must adjust their defence to the each predator and not use a general response towards all predators (Beckerman et al. 2010). Many different prey species have been found to be able to recognise various predators and to adjust their defence accordingly (McIntosh and Peckarsky 1999, Laurila 2000, Gunzburger and Travis 2005, Petrin et al. 2010). Freshwater snails are under threat from a wide variety of predators like waterfowl, fish and different invertebrate predators and have been found to induce predator specific defences. The behavioural defences found in freshwater snails range from hiding behaviours (Dewitt et al. 1999, Rundle and Brönmark 2001), shell shaking (Townsend and McCarthy 1980) to crawl-out behaviours (Alexander

Fig. 2. The crucian carp *Carassius carassius* is common in ponds and a notorious predator on snails and gammarids. This predatory fish was used in **papers I-IV**.

and Covich 1991, Dalesman et al. 2009). The morphological defences often involve different features of the shell, e.g. thickness (Bourdeau 2011), shape (Dewitt 1998) and coloration (Manríquez et al. 2009), but also the pigmentations of the mantle, as I showed in **paper II**. Hoverman (2005) showed that the freshwater snail *Helisoma trivolvis* could produce both crush-resistant shells against shell crushing predators and invasion resistant shells against shell invaders. The freshwater snail *Planorbella trivolis* can change its shell morphology so that it provides an effective defence against both crayfish and water bugs, but the shell morphology that is effective against one predator increases the susceptibility against the other and vice versa (Hoverman and Relyea 2009). Conflicting morphological shell shapes was also found in *R. balthica*, but here the snail produced an intermediate shell shape, which protects them from both predators (Lakowitz et al. 2008). In **paper III** I studied how *R. balthica* responds to multiple predators, but this time the focus was on anti-predatory behaviours and survival. In contrast to the Lakowitz et al. (2008), who studied effects of fish and crayfish, I used fish and leech as predators and there are several reasons for this. First, the two main predator regimes that snails are exposed to are presence or absence of fish, where invertebrate predators such as leeches are the dominant predators in fish-free habitats. Secondly, I was interested in the different hunting modes of these two predator types, i.e. fish vs leech. The molluscivorous fish crucian carp is an visual hunter that search for its prey (Fig. 2), while the leech *Glossiphonia complanata* is a sit-and-wait or sit-and-pursuit type of predator (Fig. 3), and, hence, these two hunting strategies should induce different defence responses and may also led to some intriguing interactions when snails are exposed to them both. The use of info-chemicals from these two predators allowed us to study the behavioural responses to these predators both when alone and in combination without allowing for any actual predation. By combining one predator with the info-chemicals of the other, it was also possible to tease apart leech and fish predation effects in a multipredator situation. Both leech and fish are efficient predators on *R. balthica*,

Fig. 3. The molluscivorous leech *Glossiphonia complanata* is common in ponds and lakes in southern Sweden. They have been found to be efficient sit-and-wait hunters, luring in refuges like rocks and macrophytes. This predator was used in **papers III** and **IV**.

but their effect is greater on juvenile snails since e.g. their morphological defences are not yet fully developed (Brown and DeVries 1985, Brönmark 1992). Hence, juvenile snails have to rely entirely on their behavioural defences. Here, I quantified two anti-predator behaviours, "refuge use" if snails where under a tile and "crawl-out" if snails climbed above the waterline in the aquarium. Snails used both these responses when exposed to fish, but when exposed to leech, snails decrease the refuge use. This is easily explained as leeches also use this refuge and hence chase snails out of this otherwise safe habitat. Interestingly, when exposed to both predators snails responded by leaving the refuge, just as they did in the leech only treatment. This response was a bit surprising at first; considering the differences in predation rate found between these predators fish should be predicted to induce a stronger response. Furthermore, based on the multiplicative model (Sih et al. 1998) I found that the calculated expected additive effect on refuge use when snails were exposed to both predators was significantly higher then the observed value in the leech + fish treatment, suggesting a multiplicative effect (Fig. 4). By ignoring the presence of fish and responding only to the leech cue, snails left the refuge and exposed themselves to fish predation, leading to an increased mortality compared to predation experiments with fish only (Fig. 2 in **paper III**). One potential explanation to this irrational decision is found in the hunting strategies of the different predators. Even though the fish have a higher predation rate, they are actively swimming around and are hence leaving a diffuse chemical trail, which reveal their presence, but not their exact position. Leech, on the other hand, is a sit-and-wait predator and the info chemicals from a sit-and-wait predator are released from one point and therefore prey may determine their physical proximity with a greater reliability and respond by leaving the refuge (Preisser et al. 2007). Invertebrate predators are in general not considered to structure snail communities the way that fish are (Hoverman et al. 2011). Nevertheless, the results from **paper III** sheds new light on this and suggest

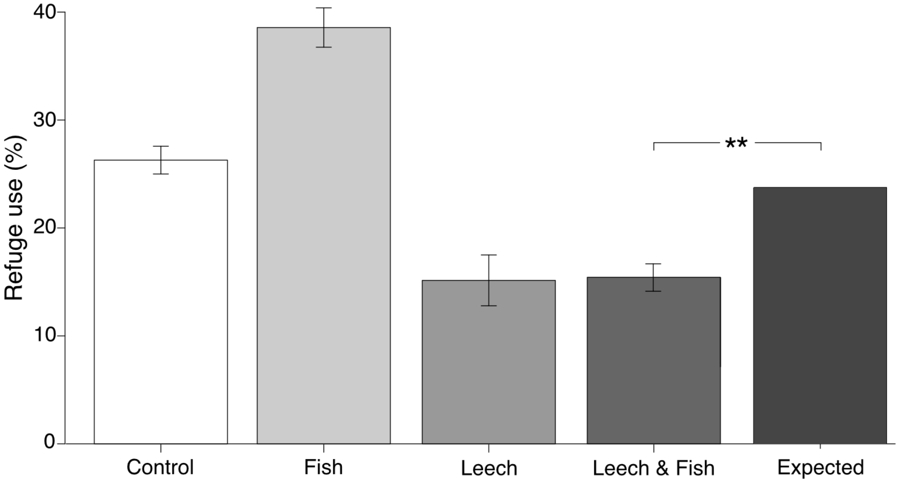

Fig. 4. Refuge use in freshwater snail *Radix balthica* exposed to control water, fish, leech or the combination of leech and fish in **paper III**. The expected value for the combined predators (based on the multiplicative model) was significantly higher then the observed value in the leech+fish treatment suggesting a multiplicative effect.

that invertebrate predators with a low consumptive rate can still have a big impact on snail communities in fish ponds. By forcing snails out of refuges, like rocks and macrophytes, invertebrate predators can indirectly play a substantial role in shaping snail communities by facilitating fish predation.

INDIVIDUAL VARIATION IN ANTI-PREDATOR DEFENCES

When studying the effects of biotic and abiotic factors on prey behaviours we often just talk about differences in the average behaviour between contexts. However, there is a lot of variation around the average and this is of course caused by an individual variation in the behavioural response. The finding that this individual variation in behaviour sometimes is consistent across time and context has led to an increase in the research associated with so-called "animal personalities". Animal personalities have been documented in a wide range of species, from invertebrates to fish to birds (Bell et al. 2009). Studies evaluating animal personality often use behavioural traits such as boldness/shyness (Ward et al. 2004), anti-predator behaviour (Quinn and Cresswell 2005), risk taking (van Oers et al. 2005), exploration (Minderman et al. 2009) and general activity levels (Kurvers et al. 2009). The most attention has been given to research of individual variation in behaviours associated with the bold-shy continuum. Individuals are here placed along this continuum by defining them as either more "bold" and hence more likely to engage in risky behaviours or as more "shy" and hence more unwilling to take risks (Wilson et al. 1994, Sih et al. 2004).

The bold-shy continuum caught my attention because it could maybe help explain the behavioural and morphological variations I found in freshwater prey exposed to predators. I modified the established refuge emergence protocol (latency to emerge from a refuge box) and were able to get consistent behavioural measurements of snail boldness by disturbing snails so they retracted into their shell and then measuring the time until they emerged again. Snails that were assessed for boldness were individually tagged with numbered bee tags (Fig. 5). The repeatability of this behaviour is high (e.g. in **paper V** repeatability was 0.64) compared to values reported in other published papers (Bell et al. 2009). In **paper IV** I categorised snails as either bold or shy and then exposed them to either fish or leech predation in experiments similar to those in **paper III.** The survival of the two personality types did not differ when exposed to leech predation, but when exposed to fish I found significant differences in survival among bold and shy snails. In contrast to my expectations I found that bold snails survived better then shy snails. Was this just an artefact from the non-natural laboratory situation or is it a reflection of predator specific selection also occurring in the wild? To investigate this I collected snails from 4 fish and 4 fish-free ponds and quantified their boldness in the lab. Intriguingly, the snails from fish ponds were significantly bolder than snails from fish-free ponds and further, snails in fish ponds had a narrower distribution of personality types with all snail having low emergence times, while snails from fish-free ponds had a wider distribution of personality types, including both bold and shy individuals (Fig. 2 in **paper IV**). Taken together, the results from **paper IV** clearly indicate that the selection pressure from predators on personality types is of great importance for the maintenance of diversity of personality types in nature.

Boldness and phenotypic compensation

The paradox that risk taking bold snails had superior survival in high-risk contexts like fish ponds raises some new questions. Do bold individuals compensate for an increased predation risk, by using complementary anti-predator defences? Trait compensations have received some attention in the past (e.g. Dewitt et al. 1999), but only a few researchers have studied the link between personality types and "phenotypic compensation" (e.g. Hulthén et al. 2014). The idea behind the phenotypic compensation hypothesis is that bold individuals need to protect themself in high-risk environments by relying more on other defences e.g. behavioural and morphological defences, than shy individuals do. To my knowledge there are only three examples of phenotypic compensation in the literature. The first relates boldness to migratory behaviour in roach and here bold roach have a higher likelihood to leave the lake for surrounding streams during winter when food is low but predation is high (Chapman et al. 2011). In another study, bold individuals of the brown anole lizards phenotypically compensated their risky life style by having a tail more suitable for autotomy (losing their tail as a defence strategy), hence, bold lizards needed less force to autotomize their tail. Finally, an example closer related to **paper IV** is that of the crucian carp, a fish known to induce a deeper body in the presence of gape size limited predators, and here Hulthén et al. (2014) found that bold crucian carp induce this morphology to a higher extent than shy individuals. This made me wonder if the same was true for *R. balthica*, i.e. that the variation found in shell shape (Brönmark et al. 2011) can be explained by personality differences. We know that freshwater snails can change their shell shape in response to predatory cues (DeWitt et al. 2000, Lakowitz et al. 2008, Brönmark et al. 2012) and that these changes in shell structure greatly reduce the attack success of predators (DeWitt et al. 2000, Auld and

Fig. 5. Snails that were assessed for boldness in **papers IV** and **V** were individually tagged with numbered bee tags.

Relyea 2011). In *R. balthica* predatory fish induces a thicker and rounder shell shape, which increases the crushing resistance of the shell (Lakowitz et al. 2008). Hence, one can predict that bold snails would invest more in these costly shell shapes (Brönmark et al. 2012) than would shy snails.

In **paper V** I tested this hypothesis. I collected egg capsules of *R. balthica* in four different ponds and after three months in the lab I then quantified their boldness and measured their shell shape. As I in **paper IV** found that fish ponds (in contrast to fish-free ponds) have very few (if any) shy individuals I collected snails from fish-free ponds, which gave us a wider distribution of snail personality types. I then categorised snails as either bold or shy and analysed shell shape outline, which gave me several principal components of which the first two made up 80% of the shell shape variation. These two principal components were associated with the roundness of the shell as well as the size of the aperture. A round shell with a big aperture is associated with enhanced crushing resistance (Lakowitz et al. 2008) and bold snails had significantly rounder shells as well as bigger apertures giving them a better protective shell than shy snails (Fig. 1 in **paper V**). One explanation for this co-variation between personality and protective shells is that bold snails are at greater risk and, thus, the selection for protective shells has been stronger than for risk-averse, shy individuals. This general pattern was found in the absence of predators, suggesting that the link between boldness and protective shells is genetically determined, revealing traces of historical predation.

CONCLUSIONS

The research in my thesis further supports the idea that predators have a strong selective force on prey phenotypes. In **paper I** we see that predator regimes can shape different fixed phenotypes of *G. pulex* and that fish predators greatly alters the behaviour and life history traits in this species. To avoid predation from fish, individuals from fish ponds pay a great cost, with increased time spent in refuge, higher non-consumptive mortality and a reduced time spend in pair formation prior to mating. However, none of these differences affected their main ecosystem service, leaf shredding. In **paper II** the freshwater snail *R. balthica* showed some really interesting responses in their mantle pigmentation, suggesting that they use disruptive coloration as a camouflage, but also that the can induce pigmentation in response to UVR as photoprotection. The behavioural and mortality results for the multi-predator situations in **paper III**, gave us new insights into the importance of non-consumptive effects and how these effects from invertebrate predators can help explain why snails densities generally are lower in fish ponds (Hoverman et al. 2011). The variance in behaviour and survival seen in **paper III** as well as in the literature was the starting point for **papers IV** and **V**. I showed in **paper IV** that the individual variance in behaviours such as activity is affected by the personality trait boldness and, furthermore, that the personality of individual snails greatly affected their chance of survival when exposed to predatory fish. In the second part I also showed that the higher survival in bold snails was reflected in the distribution of personalities in fish ponds, as a field survey showed evidence for selection for bold snail in fish ponds, but not in fish-free ponds. The variance found in *R. balthica* shell shape (Lakowitz et al. 2008) could in **paper V** to some extent also be explained by individual differences in personality. Also, I found that bold snails had a rounder shell as well as a wider aperture, two traits related to crushing resistance in this species (Lakowitz et al. 2008).

In summary, my work reveals some new insights in how predators have shaped prey phenotypes through years of selective predation. In addition to the non-consumptive effects that predators have on prey phenotypes its clear that phenotypes that are badly adapted will quickly be removed from the population. Intriguingly, I also found that predators can shape the distribution of animal personalities and give rise to phenotypic compensation, where bold individuals compensate their risky life style with more pronounced defence traits.

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