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**Závislost predace a rychlosti metabolismu na teplotě z pohledu
kořisti i predátora**

Diplomová práce

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Annotation:

Climate changes affect species interactions which can have cascading effect up to the ecosystem level. This work investigates the effects of temperature and predator size on predator-prey interactions by measuring the feeding rates of predators and metabolic rates of both predator and prey, using dragonfly larvae *Aeshna cyanea* and toad tadpoles *Bufo bufo* as a model system. Possible consequences of the findings for the impacts of climate change and predation on amphibian populations are discussed.

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V Českých Budějovicích dne 19. 4. 2017

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Cíle práce

1. Shrnout známé údaje o vlivu teplotních změn na stabilitu druhových interakcí a jejich důsledků pro potravní síť.
2. Provést laboratorní experiment za účelem změření intenzity predace a rychlosti metabolismu predátora i kořisti ve třech teplotách.
3. Získané údaje vyhodnotit pomocí moderních statistických metod.

Úvodní komentář

Klimatické změny

Globální změny v oblasti životního prostředí, zejména klimatické změny a zvyšování průměrných teplot, podtrhují důležitost zkoumání vlivů klíčových abiotických a biotických faktorů ovlivňujících nejen samotné druhy, ale i druhové interakce (Tylianakis et al. 2008; Shurin et al. 2012; Cahill et al. 2013). Tyto změny jsou považovány za hlavní ohrožení globální biodiverzity, jež může vést k vymření tisíců druhů živočichů během příštího sta let (Barnosky et al. 2011; Bellard et al. 2012).

Přímé vlivy teploty na jedince a populace

Přímé vlivy zahrnují důsledky teplotních změn působící přímo na jedince daného druhu. Zvýšení teploty může mít pozitivní vliv, neboť v určitém rozsahu teplot zrychluje metabolické procesy a vede k rychlejšímu růstu jedinců a tím i rychlejšímu populačnímu růstu (Stachowicz et al. 2002).

Mezi hlavní negativní přímé vlivy zvýšení teploty okolního prostředí se řadí zejména překročení horní teplotní hranice fyziologické tolerance druhu. Nejvíce ohrožené jsou tak zejména druhy přisedlé a druhy s omezenou termoregulací (např. tropický hmyz: Deutsch et al. 2008; plazi: Huey et al. 2009). U pohyblivých živočichů může zvýšení teplot kromě přehřátí organismu tlumit pohybovou aktivitu a zároveň zvyšovat energetické náklady, což může vést k vyhladovění organismu a následné smrti (např. varan Rosenbergův: Kearney, Shine & Porter 2009). U vodních organismů může zvýšení teploty vody způsobovat zrychlení metabolismu a tím vyšší spotřebu kyslíku jedinci, ale zároveň dochází k jejich ohrožení díky sníženému obsahu kyslíku ve vodním prostředí (např. slimule živorodá: Portner & Knust 2007).

Oteplování může působit na různé biologické procesy v rámci jednoho organismu různým způsobem (Zuo et al. 2011). Mnoho studií potvrdilo, že zvýšená teplota u ektotermů urychluje vývoj více než růst (Daufresne, Lengfellner & Sommer 2009; Forster, Hirst & Atkinson 2012) a jedinci pak dorůstají menší velikosti (tzv. *temperature-size rule*). Zatímco změny ve velikosti těla vlivem vyšší teploty bývají u terestrických organismů různé, menší velikost v dospělosti je pozorována zejména u vodních organismů (Forster et al. 2012; Horne, Hirst & Atkinson 2015), pravděpodobně v souvislosti se snižujícím se množstvím kyslíku (Atkinson, Morley & Hughes 2006).

Navíc u větších vodních druhů dochází k výraznějšímu zmenšení velikosti těla oproti menším, zatímco u terestrických je tomu naopak (Horne et al. 2015).

Nepřímé vlivy teploty na jedince a populace

Nepřímé vlivy klimatických změn se mohou projevovat ztrátou vhodných stanovišť a změnami interakcí s ostatními druhy ve společenstvu. Nedostatek srážek a vysychání způsobené vyššími teplotami může vést ke ztrátě vhodného prostředí pro ryby (Trape 2009) a jiné vodní organismy včetně skupin žijících ve vodě v určitém stádiu vývoje, např. obojživelníky (McMenamin, Hadly & Wright 2008). Ubývající vodní prostředí tak může pro některé druhy představovat vyšší riziko vyhynutí než samotné změny teploty.

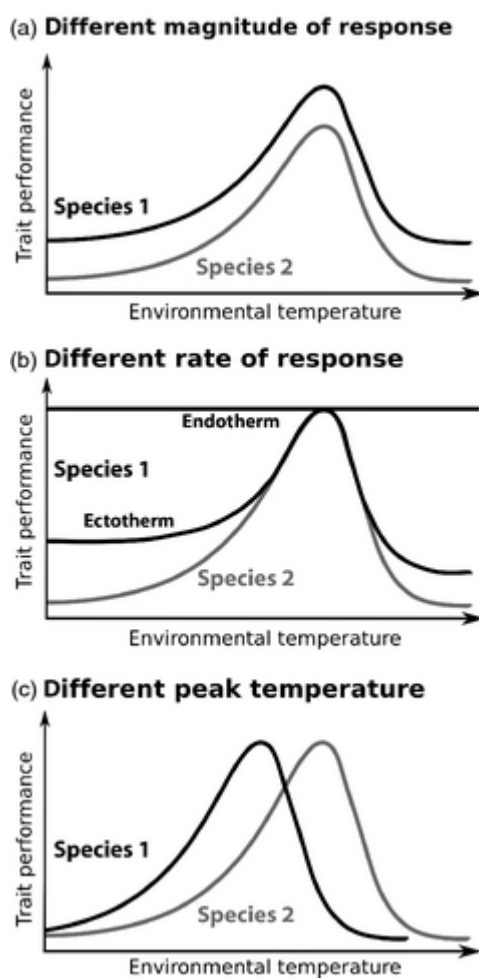
Teplotní změny mohou dále ohrožovat druhy prostřednictvím negativního vlivu na populace druhů nižších trofických úrovní, na nichž jsou závislí, jako například predátor na kořisti (Harvey & Moore 2017) či býložravec na rostlině (Schweiger et al. 2008). Stejně tak mohou teplotní změny naopak zvýhodňovat kompetitory (Wethey 2002), predátory (Harley 2011), patogeny (Pounds et al. 2006) nebo invazivní druhy (Cheng, Komoroske & Grosholz 2017) a zesilovat tak jejich negativní vliv na daného jedince či populaci druhu.

Vliv teplotních změn na mezidruhové interakce

Změny teplot ovlivňují všechny organismy. Odpovědi jedinců na teplotní změny jsou primárně fyziologické (např. změna rychlosti metabolismu či pohybu nebo odlišné strategie reprodukce), ale hrají roli i v mezidruhových interakcích. Jelikož se ale odpovědi mezi jednotlivými stadii, druhy či populacemi mohou lišit (Dell, Pawar & Savage 2011), mohou tyto rozdílné odpovědi jedinců vést ke změnám mezidruhových interakcí včetně vztahů konzument-zdroj (Gilbert et al. 2014; Sentis, Hemptinne & Brodeur 2014). Tyto interakce jsou základem potravních sítí a jejich narušení může dále způsobovat kaskádový efekt na vyšších trofických úrovních a ovlivnit tak celý ekosystém (Barton & Schmitz 2009; Rall et al. 2010; Kratina et al. 2012). Pochopení důsledků klimatických změn pro mezidruhové interakce a jejich dalekosáhlé dopady na funkci ekosystémů přesto dosud bylo věnováno relativně málo pozornosti (Vasseur & McCann 2005; Vucic-Pestic et al. 2011; Sentis et al. 2016b).

Dell, Pawar a Savage (2014) ve své studii popisují tři nejběžnější typy asymetrií v odpovědích na teplotní změny ve vztahu konzument-zdroj (Obr. 1). Prvním je rozdílná úroveň vyjádření odpovědi konzumenta a zdroje, obě ale škálují s teplotou stejně (a),

druhým rozdílná intenzita odpovědi, tj. rozdílné zvýšení či snížení intenzity odpovědi u obou druhů na změny teploty (b). Tomuto typu také odpovídá situace, kdy jeden z interagující dvojice je endotermní a na změny teploty nereaguje. Třetí typ asymetrie v odpovědích představují posunuté křivky odpovědi s rozdílnou teplotou odpovídající maximální míře odpovědi (c). Vlivem teplotních změn může k takovýmto asymetriím mezi druhy docházet častěji a k narušení interakcí může postačit již malá teplotní změna (Davis et al. 1998; Post et al. 1999; Sanford 1999).



Obr. 1: Tři obecné scénáře rozdílných reakcí na teplotu v rámci jedinců či populací.

Vliv teplotních změn na rychlost metabolismu a intenzitu predace

Oteplování může stabilizovat či destabilizovat interakce a následně dynamiku populací v závislosti na změnách v rychlosti metabolismu a příjmu potravy, které mohou vést ke změnám v poměru energetického zisku a výdeje predátora i kořisti (Vasseur & McCann 2005; Sentis, Morisson & Boukal 2015). Metabolismus je souhrn

biochemických dějů, během kterých je získaná energie a živiny přetransformována do vykonávání životních funkcí a vzniku tělesných struktur. Teplota obecně urychluje metabolické děje a s nimi se zvyšují požadavky na přísun energie (Rall et al. 2010; Vucic-Pestic et al. 2011). Příjem potravy tak většinou vykazuje podobnou závislost na teplotě jako rychlost metabolismu.

Změny rychlosti metabolismu a příjmu potravy v závislosti na teplotě a tělesné velikosti představují kontroverzní téma, které je předmětem mnoha studií (Brown et al. 2004; Glazier 2005; Sentis et al. 2014). Podle metabolické teorie ekologie škáluje rychlost metabolismu s teplotou a tělesnou velikostí s exponentem $3/4$ (Brown et al. 2004). Tento exponent potvrzují také některé další práce (Savage et al. 2004; Vucic-Pestic et al. 2011), ale současné studie spíše ukazují, že exponent $3/4$ nelze vztahovat na všechny organismy za všech podmínek, protože záleží na řadě dalších faktorů, jako je druh, stáří, velikost, aktivita či na tom, zda se jedná o endotermní či ektotermní organismus. Pozorovaný škálovací exponent bývá většinou v rozmezí hodnot $2/3$ a 1 (Glazier 2005; Niven & Scharlemann 2005; Glazier 2010; Glazier 2015).

Intenzita predace souvisí kromě teploty rovněž s mobilitou (Vucic-Pestic et al. 2011), pohybovou rychlostí (Dell et al. 2014) a poměrem tělesných velikostí (Brose et al. 2008) predátora a kořisti. Vucic-Pestic a kol. (2011) například ve své studii prokázali, že intenzita útoků střevlíků stoupá s teplotou pouze v případě, že predátor útočí na pohyblivou kořist (dospělou octomilku), zatímco četnost útoků na nepohyblivou kořist (larvy potemníka) byla na teplotě prostředí nezávislá. Vlivem oteplování dochází u pohyblivých organismů k vyšší aktivitě a častějším setkáním, respektive se zkracuje rychlost hledání kořisti (Vucic-Pestic et al. 2011; Dell et al. 2014). S teplotou a tělesnou velikostí predátora se zkracuje rovněž doba zpracování kořisti predátorem (Garcia-Martin et al. 2008; Vucic-Pestic et al. 2011), která se ale naopak prodlužuje s tělesnou velikostí kořisti (Vucic-Pestic et al. 2010).

Řada studií (např. Aljetlawi, Sparrevik & Leonardsson 2004; Vucic-Pestic et al. 2010) popisuje unimodální vztah mezi intenzitou predace a poměrem tělesných velikostí predátora a kořisti. Zatímco četnost útoků se zvyšuje s velikostí predátora (větší predátor například dále dohlédne než predátor menší), úspěšnost ulovení se s velikostí predátora snižuje, pakliže dojde k překročení optimálního poměru tělesných velikostí predátora a kořisti (Aljetlawi et al. 2004; Brose et al. 2008). Důvodem pro nízkou úspěšnost lovu může být rovněž menší motivace predátora lovit malou kořist (Petchey et al. 2008).

Vedle vlivu teploty na rychlost metabolismu a příjem potravy je podstatné rovněž zkoumání energetické účinnosti predátora, neboli poměru získané a vydané energie (Binzer et al. 2012; Sentis et al. 2015). Rychlost metabolismu a příjem potravy totiž nemusí na teplotě záviset stejně. V některých případech dochází vlivem oteplování k rychlejšímu metabolismu a zároveň nižšímu příjmu potravy predátora. Poté ale predátor nemusí pokrýt své energetické požadavky, což může vést k jeho hladovění a případně vyhynutí celé populace (Petchey et al. 1999; Vucic-Pestic et al. 2011). Měření energetické účinnosti je proto důležité pro zkoumání síly druhových interakcí a jejich důsledků pro stabilitu potravní sítě a ekosystému (Berlow et al. 1999).

Vliv teploty a dostupnosti potravy na vyjádření fenotypové plasticity

Z fyziologického hlediska je vliv teploty prostředí a dostupnosti potravy důležitý rovněž pro využití schopnosti fenotypové plasticity u kořisti i predátora, zejména je-li mezi nimi rozdíl ve velikosti. V reakci na intenzitu predace může kořist měnit své morfologické vlastnosti tak, aby se stala pro predátora méně výhodná, a predátor tak, aby mohl snáze konzumovat i větší kořist (Kopp & Tollrian 2003; Kishida, Mizuta & Nishimura 2006; Edgell & Rochette 2008; Kishida et al. 2010).

Zvýšená teplota může zvýšit intenzitu predace, a tím nepřímo zvyšovat potřebu obranného fenotypu u kořisti (Laurila, Lindgren & Laugen 2008; van Uitregt, Hurst & Wilson 2013). Morfologické změny či změny v chování (např. snížená aktivita či agregační chování) sice riziko predace snižují, ale současně mohou zpomalit růst a vývoj a snížit tak šanci na přežití kvůli nižšímu příjmu energie (Tollrian & Harvell 1999; Van Buskirk 2000; Stav, Kotler & Blaustein 2007). Pro vyjádření obranného fenotypu kořisti vůči predaci je tak podstatná dostupnost potravy. Zatímco dostatek zdrojů může vyjádření obranného fenotypu kořisti posílit, omezené zdroje mohou naopak zpomalit růst a vývoj kořisti a tím riziko predace zvýšit (Werner & Anholt 1993; Van Buskirk 2000; Bennett, Pereira & Murray 2013).

Intenzitu predace dále nepřímo ovlivňuje změna tělesné velikosti predátora nebo kořisti s teplotou, zejména u vodních organismů (Atkinson et al. 2006), neboť poměr velikosti predátora a kořisti určuje intenzitu predace (Brose et al. 2008; Boukal 2014) a tím nepřímo ovlivňuje stabilitu potravních sítí (Sentis et al. 2016a).

Vliv teplotních změn na intenzitu predace a fenotyp u obojživelníků

Významnou skupinu z hlediska ohrožení nejen globálním oteplováním představují obojživelníci. Jedinečnou skupinu v rámci čtyřnožců z nich dělá složitý životní cyklus a fenotypová plasticita, respektive schopnost odpovědi larev na podmínky prostředí (Wells 2007; Denver 2009; Enriquez-Urzelai et al. 2013).

Pro evoluci fenotypové plasticity obojživelníků je podstatná heterogenita prostředí. Typickými příklady heterogenního prostředí jsou mělké rybníky a jiné menší vodní plochy charakteristické pravidelnými změnami výšky vodní hladiny, kde vysychání představuje pro larvy obojživelníků největší ohrožení (Newman 1992; Loman & Claesson 2003). Fenotypová plasticita ve smyslu urychlení vývoje v důsledku vysychání vody je známa u mnoha druhů obojživelníků (např. *Bufo calamita* (Tejedo & Reques 1994), *Hyla gratiosa* (Leips, McManus & Travis 2000), *Rana temporaria* (Laurila & Kujasalo 1999)). V těchto systémech je pro obojživelníky přechod z vodního prostředí v odpovídající velikosti a stáří rozhodující pro následující život na pevnině (Rowe & Ludwig 1991).

S vysycháním vodního prostředí souvisí dále také vyšší hustota predátorů a tedy vyšší riziko predace. Dravý vodní hmyz, zejména larvy vážek, jsou efektivními predátory larev obojživelníků a představují tak významné riziko pro jejich přežití, zejména v dočasných vodách a nádržích bez ryb. Jejich vzájemné interakce jsou široce studovány (Caldwell, Thorp & Jervey 1980; Travis, Keen & Juilianna 1985; Semlitsch 1990). Četnost setkání pulců a číhajícího predátora, například již zmíněné larvy vážky, je dána zrakovými schopnostmi predátora a různými pohybovými schopnostmi pulce (Chovanec 1992). Woodward (1983) vysvětlil zvýšené ohrožení predací pulců druhů žijících v dočasných vodních prostředích jejich neustálým pohybem a tedy vyšším vystavováním se riziku predace, zatímco pulci druhů žijících v permanentních vodních prostředích se pohybují spíše sporadicky. Neustálá pohybová aktivita pulců rodu *Bufo* (včetně *B. bufo*) z nich dělá snadnou kořist pro larvy vážek (Heyer, McDiarmid & Weigmann 1975; Lawler 1989). Ačkoliv toxicita ropuch je významnou obranou proti mnoha predátorům (Wassersug 1971), vůči bezobratlým predátorům je neúčinná (Chovanec 1992).

V případech ohrožení predací larvy obojživelníků snižují svoji aktivitu a doba jejich vývoje se prodlužuje na rozdíl od urychlení vývoje během vysychání vody (Ball & Baker 1996; Laurila, Kujasalo & Ranta 1998). Kombinovaný vliv zvýšených teplot (resp. rizika vysychání) a rizika predace na fenotyp larev obojživelníků byl testován například u pulců *Rana temporaria* (Laurila & Kujasalo 1999), kteří více reagovali na úbytek vody než na přítomnost larvy vážky a vývoj urychlovali. Nicméně vliv zvýšené

teploty a rizika predace na mortalitu larev obojživelníků zatím nebyl studován. Lze ale předpokládat, že zvyšující se intenzita predace vlivem vyšší teploty bude mít i přes schopnost larev obojživelníků urychlovat svůj vývoj významnější dopad na jejich populace vyjma případů, kdy teplota překročí horní letální práh nebo povede k vyschnutí stanoviště před dokončením jejich vývoje.

Shrnutí

Klimatické změny a dostupnost zdrojů mají významný dopad nejen na jednotlivé druhy, ale i na jejich vzájemné interakce a v důsledku toho na populace a celé ekosystémy. Zvýšená teplota působí na organismy přímo skrz základní procesy ovlivňující příjem a zpracování energie, zejména rychlost metabolismu a příjmu potravy. Díky rozdílným reakcím na teplotní změny mezi predátorem a kořistí může docházet k narušení jejich interakcí a následně ke změnám v potravních sítích. Zatímco řada studií se zabývala vlivem teploty a tělesné velikosti na rychlost metabolismu či příjem potravy jednotlivých druhů, společná závislost predátora i kořisti byla studována zatím jen okrajově. Zkoumání toho, jak různé faktory prostředí ovlivňují vlastnosti jedinců a tím i jejich vzájemné interakce, je přitom důležité stejně jako odpovědi jednotlivých druhů na změny prostředí.

Úkolem předkládané experimentální studie bylo ve třech teplotních režimech zjistit vliv teploty na rychlost metabolismu predátora i kořisti a to, jak teplota a tělesná velikost predátora ovlivňují intenzitu predace. K tomuto účelu jsem použila larvy vážky *Aeshna cyanea* jako predátora a pulce ropuchy *Bufo bufo* jako kořist. V souladu s dalšími studii jsem očekávala, že (1) ve vyšší teplotě budou mít larvy vážky i pulci rychlejší metabolismus a zvýší se intenzita predace a (2) intenzita predace a celková mortalita kořisti zahrnující i letální zranění způsobená predátorem poroste spolu s velikostí predátora. Dále jsem se zaměřila na případné rozdíly ve škálování rychlosti metabolismu a intenzity predace s teplotou a tělesnou velikostí predátora, což by mohlo vést k predátorově nižší energetické účinnosti a riziku hladovění. Tyto rozdíly jsem zkoumala především v rámci jednotlivých instarů predátora. Vzhledem ke schopnosti pulců urychlit vývoj vlivem vyšší teploty jsem také srovnala, jak rychlost jejich metabolismu škáluje s teplotou v porovnání s intenzitou predace.

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**Temperature dependence of predation and metabolic rates:
a combined predator and prey perspective**

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Summary

1. Increasing temperatures influence individuals and species interactions, which can destabilize population dynamics and lead to cascading ecosystem effects. It is thus important to understand how temperature alters species interactions and energy budgets of consumers and their resources to predict the impacts of global warming on community dynamics.

2. We experimentally investigated the impact of temperature on the predation and metabolic rates of predator and on the overall mortality (including both eaten and fatally injured individuals) and metabolic rates of the prey, using larvae of the dragonfly *Aeshna cyanea* and *Bufo bufo* tadpoles as a model system. To evaluate the size dependence of feeding and metabolic rates of the predators, we used three last instars of the dragonfly larvae. We ran short-term experiments to measure predation rates and prey mortality and measured standard respiration rates in short-term trials as a proxy for metabolic rate.

3. Temperature had a significant effect on the intensity of predation, prey mortality, and metabolic rates of both predator and prey. Feeding rates of dragonfly larvae and prey mortality increased with temperature and predator size across all predator instars. Surprisingly, feeding rates and prey mortality decreased with predator size within instars. Metabolic rates of predators and prey also increased with temperature and size, but the size scaling differed between predators and prey and within predator instars. While the scaling exponent of tadpoles was close to 0.75, the exponents within each dragonfly larval instar were much steeper and consistent with isometric or even supra-isometric scaling.

4. The results indicate higher developmental costs of dragonfly larvae, especially in the penultimate instar. These costs are covered by elevated predation rates early in each instar, which implies that details of species ontogeny can substantially alter the currently used standard models of size- and temperature-dependent predator-prey interactions.

5. Moreover, global warming and predation risk are ubiquitous threats to amphibians worldwide. Our results contribute towards more accurate predictions of the effects of climate change on survival of amphibians and predator-prey interactions in structured populations.

Key-words: amphibians, aquatic insects, climate change, feeding rate, food webs, ontogeny, predator-prey interactions, scaling

Introduction

Climatic changes, especially increased global temperature, and changes in food enrichment are the most important factors influencing biodiversity of species (Sala et al. 2000; Nelson 2005; Binzer et al. 2012). Nearly all metabolic and biological processes are sensitive to temperature (Brown et al. 2004), and exceeding the upper thermal limit can even lead to extinction of some species (Thomas et al. 2004; Cahill et al. 2013) and consequently threaten persistence of whole communities. Therefore, it is not sufficient to observe responses to climate changes only in individual species, but focus on interactions among species as well (Dunson & Travis 1991; Davis et al. 1998).

Trophic interactions, including predator-prey links, represent the most common interaction type in freshwater communities. They determine the flux of energy and materials towards higher trophic levels as well as across communities and ecosystems. Interacting individuals can respond to climate change differently and the responses can differ between life stages, populations and species (Dell, Pawar & Savage 2011, 2014). This means that even a slight temperature change can generate cascading effects to other trophic interactions across the food web (Post et al. 1999; Sanford 1999; Tylianakis et al. 2008). Thus, temperature can indirectly influence structure and dynamics of ecosystems including food web stability (Yvon-Durocher et al. 2011; Binzer et al. 2012; Nelson, Bjornstad & Yamanaka 2013).

To predict the consequences of warming on interaction strengths and subsequently the stability of ecosystems and biodiversity, it is important to understand how temperature changes affect biological rates, especially feeding rates (i.e., energy gain) and metabolic rates (energy loss; Vasseur & McCann 2005; Rall et al. 2010) of both predators and prey. For example, warming can increase predator consumption rates due to higher demands for energy (Rall et al. 2010; Vucic-Pestic et al. 2011) that can lead to reduction of resources (top-down effect; Anderson et al. 2001; O'Connor et al. 2009; Hoekman 2010). On the other hand, acceleration of predator metabolism combined with limitation of resources can conversely lead to growth restriction and extinction risk of consumers (bottom-up effect; Rall et al. 2010; Vucic-Pestic et al. 2011).

Some studies (Rall et al. 2010, 2012; Vucic-Pestic et al. 2011) showed that metabolic rates increase more strongly with temperature than feeding rates. This decreasing energetic efficiency can lead to starvation and even to extinction of consumers (Petchey et al. 1999; Rall et al. 2010; Rall et al. 2012). Further, prey can grow faster and

escape predation by reaching a size refuge (Costa & Kishida 2015). Thus, temperature and food availability together impact pairwise interactions and food web stability. However, this impact is not sufficiently explored (Hoekman 2010; Shurin et al. 2012; Sentis, Hemptinne & Brodeur 2014).

Thermal conditions are particularly important for predator-prey interactions involving ectotherms such as amphibians (Anderson et al. 2001) and insects (Thompson 1978). Ectotherms are vulnerable to warming because their physiological functions (e.g., activity, growth rate, reproduction) directly depend on temperature of environment in contrast with endotherms, which can maintain constant body temperature (Frazier, Huey & Berrigan 2006). Recent studies of terrestrial ectotherms (Thomas et al. 2004; Tewksbury, Huey & Deutsch 2008) show that physiological impacts of higher temperature often decrease with latitude, and tropical or subtropical organisms are most threatened by climate warming. Tropical species have narrower thermal tolerance to temperature than species at higher latitudes because they live close to their optimal temperature (Deutsch et al. 2008; Huey et al. 2009; Duarte et al. 2012).

Thermal response curves of biological rates of ectotherms are in general unimodal and organisms typically experience a wide temperature range between their minimum critical temperature and peak temperature, at which the trait value becomes maximized (Huey & Berrigan 2001). The response curve is usually asymmetric with shallower slope in the increasing part and highly negative slope beyond the optimum temperature (Dell et al. 2011) due to rapidly inhibited metabolic processes (Ratkowsky, Olley & Ross 2005) or oxygen limitation in aquatic environments (Portner & Knust 2007). However, most studies focus on the rising part of thermal response curve (Savage et al. 2004; Deutsch et al. 2008) that is important for understanding initial responses to warming.

Asymmetries in thermal responses of interacting species can cause changes in predator-prey dynamics. Dell et al. (2014) described three general scenarios that can affect consumption rate: differences in the levels of performance of the response of consumer and resource, differences in rates of response, and differences in temperature for peak performance. Moreover, these asymmetries can be stronger due to climatic changes, as species change their geographical distributions and phenology. Although feeding rates and other biological rates depend on predator and prey body masses and environmental temperature, the exact scaling relationships are often unknown (Rall et al. 2012). For example, Smolinsky and Gvozdik (2014) investigated activity levels of newt larvae as prey and dragonfly larvae as predators when exposed to thermal stress. While predators

increased activity levels in rising temperatures, prey responded by reduced movement, possibly due to predator avoidance or physiological limitations.

Intensity of predation can also be influenced by phenotypic plasticity in behavioural, morphological, physiological and life-history traits of both predator and prey (Kishida et al. 2014). This complicates the assessment of temperature impacts on consumption rates. For example, increased temperature can accelerate predator growth rates as well as shorten their searching and handling time and consequently increase consumption rates. However, prey can evolve various strategies to avoid predation, such as improved escape ability (Anderson et al. 2001; Vucic-Pestic et al. 2011; Sentis et al. 2014). These adaptive responses to environmental changes, including higher predation risk, play important role for size-dependent predation when intensity of predation is determined by factors influencing both predator and prey growth (Cohen et al. 1993; Anderson et al. 2001; Kishida, Trussell & Nishimura 2009; Costa & Kishida 2015).

Predator-amphibian interactions are subject of many studies focusing on predator-prey interactions (e.g., Travis, Keen & Juilianna 1985; Semlitsch 1990) but the impact of climate change on their interactions is little explored. To fill this gap, we experimentally investigated effect of temperature on intensity of predation and metabolic rate both predator and prey in three temperature regimes using larvae of the dragonfly *Aeshna cyanea* (Odonata: Aeshnidae) as predators and toad *Bufo bufo* (Anura: Bufonidae) tadpoles as prey. Amphibian-insect interactions provide a useful model system to study the responses of predator-prey interactions to changing temperatures in freshwater ecosystems (Smolinsky & Gvozdik 2014). Predatory aquatic insects, including dragonfly larvae or water bugs, are effective natural enemies of tadpoles (Caldwell, Thorp & Jervey 1980). Moreover, *Bufo* tadpoles are palatable to some aquatic insect predators including dragonfly larvae (e.g., *Pantala flavescens*, Heyer, McDiarmid & Weigmann 1975; *Aeshna cyanea*, Chovanec 1992) and their continual and slow movement makes them greatly visible and easy prey for dragonfly larvae as compared to, e.g., *Rana* tadpoles (Chovanec 1992; Alvarez & Niecieza 2006).

We expected that predator feeding rates and both predator and prey metabolic rates will increase allometrically with temperature and predator body mass according to the scaling predicted by the theory of metabolic ecology. We compared if the body mass and temperature scaling was the same for both predation and metabolic rates or not, leading to dependence of predator energetic efficiency on body size or temperature. From the prey perspective, we compared if the metabolic rate (as a proxy for developmental rate) scaled

differently than predation with temperature, which could indicate the existence of thermal optima in a food-web context for the tadpoles.

Material and Methods

Laboratory experiments

Experiments were carried out from 11 June to 8 July 2015 in the laboratory at the Department of Ecosystem Biology, Faculty of Science, University of South Bohemia in České Budějovice, Czech Republic. The experiments were carried out in temperature-controlled incubators (Lovibond BSK ET 650) at three temperatures, hereafter referred to as 15, 20 and 25°C (mean \pm SD: 15.5 \pm 0.36°C, 20.4 \pm 0.36°C, 25.2 \pm 0.35°C, respectively) and 18L:6D photoperiod.

Larvae of *Aeshna cyanea* were collected in a forest pond near the village of Zliv, Czech Republic, and tadpoles of *Bufo bufo* were collected in a small pond in České Budějovice, Czech Republic. We used three larval stages of *Aeshna* (F-2, mean \pm SD dry weight: 0.039 \pm 0.004 g; F-1, 0.070 \pm 0.010 g; F-0, 0.125 \pm 0.015 g; see below for details of weighing and wet-to-dry weight conversion). The tadpoles (dry weight: 0.020 \pm 0.006 g) were at mean Gosner stage 36 (range 35–37) (Gosner 1960) at the start of the experiment.

Before the experiments, dragonfly larvae were acclimated individually in plastic cups filled with 0.1 L of aged tap water and a piece of peat moss (*Sphagnum* sp.) in a temperature-controlled room (19.0 \pm 0.5°C, 16L:8D photoperiod) and fed for at least two days daily *ad libitum* with mosquito larvae and tubifex worms. Tadpoles were kept together in large plastic boxes with aerated water at 20°C (18L:6D photoperiod) and fed with TROPICA flake food for fish (Dajana pet, Czech Republic).

Experiment 1. Effect of temperature and predator size on intensity of predation

Before the start of the experiment, larvae of dragonfly were starved and acclimated for 24 hours at the experimental temperature in the incubators. Every larva was kept individually in a plastic cup filled with 0.1 L aerated tap water aged for at least 24 hours with a stripe of green plastic mesh and a piece of *Sphagnum* sp.

As experimental arenas, we used transparent plastic jars (width x length: top 12.0 x 17.0 cm, bottom 10.0 x 14.5 cm, height 12.5 cm) filled with 1.5 L of min. 24 hours aged aerated tap water, with ca. 1 cm of fine crystalline sand (diameter < 1 mm (Sentis, Morisson & Boukal 2015) on the bottom and two pieces of plants with four leaves (length 16 cm, width 2.3 cm) made of a green plastic fabric (mesh size ca. 3 mm) and fixed with a small stone (diameter ca. 2 cm). We first introduced eight tadpoles as prey and then (after ca. 5 minutes) one dragonfly larva to each experimental arena. Mortality of tadpoles was

assessed after 24 hours and their natural mortality was measured in controls without dragonfly larva. Each dragonfly larva was gently dried with a cotton pad and weighed to the nearest 0.0001 g using the Kern ABJ 120-4M (Kern & Sohn, Germany) balance at the end of the experiment. We did not weight the larvae before the experiment to minimize the effect of handling on their feeding performance. Wet weights (w) were converted to dry weight (dw) using the species-specific allometry $dw = 0.162 w^{1.02}$ based on previously measured individuals (Boukal et al. unpublished data). We performed eight replicates for each dragonfly instar and eight controls without predator in each temperature.

To account for variation in the amount of ingested prey on the weight of predators assessed after the predation experiment, we ran an additional feeding experiment to quantify the weight gains of the predators as a function of the number of ingested tadpoles. We used F-1 larvae ($n = 44$), which were starved and acclimated 24 hours in temperature-controlled room with diffuse daylight ($20^{\circ}\text{C} \pm 0.5^{\circ}\text{C}$, 16L:8D photoperiod). The experiment ran for 12 hours (8 a.m. to 8 p.m.) at 20°C in daylight conditions in the same room. Transparent plastic arenas (width x length: top 8.5 x 10.2 cm, bottom 6.0 x 7.8 cm, height 8.3 cm) were filled with 0.4 L of aged tap water and with a stripe of green plastic mesh and a piece of *Sphagnum* sp. Each dragonfly larva was gently dried with a cotton pad and weighed to the nearest 0.0001 g as above before the start of the experiment. During the experiment, each larva was fed one tadpole at a time. Immediately after consumption, they received another tadpole and all fecal pellets of the larvae and uneaten remains of the prey were removed. Dragonfly larvae were gently dried and weighed again after the end of the experiment. All prey remains and fecal pellets were frozen at -20°C and subsequently dried at 60°C for 24 h, and weighed to the nearest 0.0001 g to obtain their dry mass. Three larvae moulted during this experiment and were removed from the data. Background weight changes were assessed in F-1 instar larvae that we kept the same way for 12 hours but not fed any tadpoles ($n = 15$).

Experiment 2. Effect of temperature and body size on predator and prey metabolic rates

We measured respiration rate, which correlates with metabolic rate (Glazier 2005). Before the start of the experiment, larvae of dragonfly and tadpoles were starved and acclimated 48 hours in the same way as in Experiment 1. Dragonfly larvae that moulted during acclimation were excluded. We measured respiration in sealed glass chamber (mean \pm SD volume: 281.2 ± 1.6 mL) with a copper grid (to provide support for the dragonfly larvae) and a small magnetic stirrer. Each chamber was filled with distilled

aerated water that was conditioned by adding purified salt (Sera©, 0.14 g L⁻¹) to achieve the conductivity of ca. 200 µS cm⁻¹ representative of field conditions in natural habitats of both species (Sentis et al. 2015) and placed for 12 hours in temperature-controlled incubators as in Experiment 1 to achieve required temperatures. Before every measurement, all equipment (bottle for the conditioned water, pots, sieve, magnetic stirrers, copper grids, glass chambers for measuring of metabolism with glass plugs) were sterilized with boiling water.

Initial concentration of oxygen was measured just before the introduction of a dragonfly larva or tadpole. After introduction, glass chambers were immediately sealed with a glass plug and placed back in the incubator. Final oxygen concentration was measured after 5 hours at 15°C, 4 hours in 20°C and 3.5 hours in 25°C. These differences were necessitated by the need to achieve measurable but not excessive oxygen depletion (mean ± SD = 0.074 ± 0.048 ml h⁻¹) across all temperatures and predator and prey individuals that differed substantially in size (see above).

Before each measurement, water in chambers was always mixed for 1 minute by a magnetic stirrer. Oxygen concentrations were measured using the Unisense© MicroOptode oxygen probe with the software SensorTrace Basic v3.2.3 (Unisense©). After the experiment, each dragonfly larva was dried with a cotton pad and weighed as in Experiment 1. Tadpoles were put to death in accordance with project permit 39/2014 and frozen to obtain dried mass. We performed 11–35 replicates for each species/instar at each temperature (Table S1). Background depletion of oxygen was assessed in 1–4 controls at each temperature every day (total 22–24 controls per temperature).

Statistical analyses

Experiment 1. Effect of temperature and predator size on intensity of predation

Effect of size of predator and temperature on intensity of predation and probability of prey mortality were analysed with a binomial GLM model with probability of predation after 24 hours as the response variable and temperature (categorical, which covers both linear and quadratic response to temperature) and predator instar (categorical) and initial dry weight (continuous, log₁₀-transformed prior to analysis) as explanatory variables. Initial dry weight was calculated by subtracting expected mean weight gain during the experiment (see below) from the final dry weight, which was calculated from the final wet weight as explained above.

We started with a full model including all explanatory variables and their interactions and performed stepwise selection based on AIC criterion (Burnham & Anderson 2002) to select the most parsimonious model. For calculation of feeding rates, we used the number of tadpoles completely eaten by the predator during experiment. Because tadpoles do not survive injuries (D. Modrá pers. observ.), we included killed or fatally injured tadpoles in the calculation of overall prey mortality. All tadpoles survived in control treatments without the predator and we thus used raw data in the analyses.

Dependence of mean predator weight gains on the number of ingested tadpoles was analysed with linear regression. In this analysis, final weight of each larva was corrected by adding the fecal pellet weight and the number of eaten tadpoles was corrected by subtracting the dry weight of uneaten remains divided by the average dry weight of a tadpole. We removed outliers ($n = 4$) which were apparently caused by errors during the weighing procedure (e.g., if the larva did not release all water from the branchial chamber during one of the measurement).

Experiment 2. Effect of temperature and body size on predator and prey metabolic rates

The effect of temperature, identity and weight on metabolic rate of predator and prey was analysed with linear regression with log-transformed body weight and oxygen depletion. Oxygen depletion in the controls was low (mean \pm SD = 0.0004 ± 0.0025 ml h⁻¹) and did not differ significantly between days and temperatures (details not shown). We thus subtracted mean oxygen depletion in the controls from the final oxygen concentration in each replicate to correct for possible background depletion of oxygen. Three outliers with extremely low oxygen consumption of two larvae in 15°C (one F-1 and one F-0 *Aeshna* larva) and one tadpole with extremely high oxygen consumption at 20°C were excluded from the data together with two F-2/F-1 *Aeshna* larvae at 25°C, which we could not assign unambiguously to instar.

All statistical analyses were performed using R software, version 3.3.2 (R Development Core Team 2016).

Results

Experiment 1. Effect of temperature and predator size on intensity of predation

Analysis of the dependence of predator weight gains on the number of ingested tadpoles after 12 hours indicated a linear relationship between mass gain of predator and number of eaten tadpoles (intercept: estimated mean \pm SE = 0.001 ± 0.003 , $t = 0.14$, $P = 0.89$; slope: 0.029 ± 0.004 , $t = 7.99$, $P < 0.0001$). That is, the larvae gained ca. 0.029 g wet weight per eaten tadpole and predator weight loss due to starvation was negligible (Fig. 1).

Probability of predation after 24 hours was significantly affected by temperature, instar and initial weight of the predator. Moreover we found a significant interaction between temperature and weight (Table 1). Probability of predation increased with temperature for each instar. Similarly, intensity of predation increased with instar at each temperature. However, we found different size- and temperature-dependent responses within instars. Predation probability decreased with body mass but not the same way in all instars. Predation pressure of F-2 larvae was independent of temperature, but the results indicated that that F-1 and especially F-0 larvae fed less at 15°C in comparison to 20 and 25°C (Fig. 2).

These results were mirrored in total prey mortality including eaten, killed and injured tadpoles, which was also significantly affected by temperature, instar, predator weight, and interaction between temperature and weight (Table 2). While mortality increased with increasing temperature and instar, we found the same different size- and temperature-dependent responses in total prey mortality within instars (Fig. 3).

Experiment 2. Effect of temperature and body size on predator and prey metabolic rates

Identity (species/instar; $F_{3,253} = 490.8$, $P < 0.0001$), temperature ($F_{2,253} = 190.3$, $P < 0.0001$), dry weight ($F_{1,253} = 132.2$, $P < 0.0001$), interactions between identity and dry weight ($F_{3,253} = 6.2$, $P = 0.0004$) and interaction between identity and temperature ($F_{6,253} = 3.6$, $P = 0.0018$) significantly affected oxygen consumption of predators and prey.

Separate analyses of the predator and prey data showed that the effects of temperature and body size differed between both species and between instars in *Aeshna* (Table 3). While the slope of the relationship between body mass and respiration rate was very close to 0.75 in tadpoles as predicted by metabolic ecology (Table 4), the analysis revealed isometric or even supra-isometric scaling of respiration rate with body mass in the

dragonfly larvae, particularly in F-1 instar (Fig. 4), in which the confidence intervals of the slope estimate no longer overlapped with the theoretically predicted value of 0.75. Temperature dependence of oxygen consumption differed slightly between predators and prey but was similar across all dragonfly instars (Table 4).

Discussion

Temperature affects biological rates and consequently species interactions (Dell et al. 2014; Gilbert et al. 2014). It is therefore important to understand its role in the impact of global changes on ecological communities. Previous studies investigated the effects of temperature on feeding rates (Rall et al. 2012), metabolic rates (Liu & Ban 2017) or both (Brose et al. 2008; Rall et al. 2010; Iles 2014). We tested impact of temperature on feeding rates and metabolism of both predator and prey, which can further help our understanding of food web complexity.

Mass- and temperature-dependent metabolic rates in predators and prey

According to the metabolic theory of ecology (hereafter: MTE), metabolic rate, feeding and growth scales with organism body mass with an exponent of close to 3/4 and increase exponentially with temperature (Brown et al. 2004). This allometric scaling of metabolism with body mass is supported by many studies (Savage et al. 2004; Rall et al. 2010; Vucic-Pestic et al. 2011). However, Glazier (2005, 2010, 2015) argues that 3/4-power scaling law is not universal, and that the value of the exponent may extensively differ across taxonomic groups (mostly between 2/3 and 1) and even more so within species. For example, the mean intraspecific metabolic scaling exponent of vertebrates is about 2/3 (Glazier 2005). Across species, the metabolic scaling exponent in endotherms is significantly less than 3/4 and closer to 2/3 (mammals: mean \pm 95% CI = 0.68 ± 0.013 , birds: 0.64 ± 0.03) compared to ectotherms in which it is usually larger than 3/4 (amphibians: 0.88 ± 0.05 , reptiles: 0.76 ± 0.04 , fish: 0.88 ± 0.06 ; White, Phillips & Seymour 2006). However, the value of the scaling exponent varies among species and life stages of the same species, often with steeper scaling exponent (close to 1) in larvae and juveniles as in, e.g., *Oncorhynchus mykiss* (larvae and young juveniles: mean \pm SE = 0.97 ± 0.019 , older juveniles and adults: 0.78 ± 0.046 ; Post & Lee 1996).

Mean intraspecific metabolic scaling exponents of invertebrates also differs from 0.75 despite a wide variability among taxa and life stages (Glazier 2005). In insects, it was investigated in a number of terrestrial species, but studies for aquatic taxa are lacking. Data for terrestrial taxa suggest that complex changes in morphology and physiology and rapid development of larvae may or may not associated with steep increase in metabolic rates. For example, honeybee (*Apis mellifera*) larvae increase their body mass more than 400-fold during 4 days and their mean metabolic scaling exponent is 0.9 (Petz, Stabentheiner &

Crailsheim 2004). Within-instar mass-scaling exponent in *Schistocerca americana* grasshoppers varies between 0.45 and 0.91 among instars (Greenlee & Harrison 2004b), but is close to 0.75 (0.73) when calculated across the entire development (Greenlee & Harrison 2004a).

In broad agreement with MTE (Savage et al. 2004; Deutsch et al. 2008), metabolic rates of tadpoles and all dragonfly larvae instars in our experiment increased with temperature. This suggests that they were within their respective ranges of suitable temperatures between the thermal minimum and peak temperature (Deutsch et al. 2008). Our results and observations of temperatures in the field (D.S. Boukal, unpubl. data) further suggest that the highest temperature used in our experiment (25°C) could be close to the peak temperature of both species.

The observed mass scaling of oxygen consumption in tadpoles (mean exponent \pm SE: 0.77 ± 0.17) was very close to the theoretically expected value of 0.75. However, mass-corrected respiration rates in the dragonfly larvae were independent of body size (F-2, F-0 instars) or even tended to increase with body size (F-1 instar). This suggests that respiration rates of dragonfly larvae accelerate towards the end of each instar, as the individuals approach moulting. Our results corroborate the finding of instar-dependent metabolic rates as in Greenlee & Harrison (2004b) but the observed mass scaling exponents in *Aeshna* were higher than in *Schistocerca* (Greenlee & Harrison 2004b) and much higher than in juvenile *Oncorhynchus mykiss* (Post and Lee 1996).

Mass- and temperature-dependent feeding rates

Both metabolic and feeding rates tend to increase with temperature (Sentis, Hemptinne & Brodeur 2012; Iles 2014), but only below the thermal maximum corresponding to the peak trait performance. For example, predation rates of many active foragers increase with temperature because predators are able to search and handle prey faster than at colder temperatures (Rall et al. 2012; Sentis et al. 2012). Dell et al. (2014) suggested that searching efficiency of predators also depends on the velocity of both predator and prey, and simultaneously higher velocity of both due to increasing temperature causes higher encounter probabilities. Because we used relatively small experimental arenas, we assume that the effect of increasing temperature on search rates of the dragonfly larvae was negligible in comparison to the effect on handling time. Increasing intensity of predation at higher temperatures in our experiment thus probably

stems primarily from faster processing and digestion of prey at higher temperature (Sentis et al. 2013, 2015). This result is in qualitative agreement with MTE.

Feeding rates also scale with predator-prey body mass ratio (Vasseur & McCann 2005; Brose et al. 2008). The relationship in most predators appears to be hump-shaped, reflecting constraints on predator feeding rates by relative size of prey, predator ability to find and pursue small prey, and energetic profitability of small prey (Brose et al. 2008; Vucic-Pestic et al. 2010; Rall et al. 2010, 2012). We used undefended prey of about the same size to remove any effect of prey size.

Consistent with previous theory and empirical observations, we found that feeding rates of dragonfly larvae increased with body size as they were higher in later instars. However, feeding rates decreased with body mass within F-2 and F-1 larvae. This very likely stems directly from higher activity and increased need for nutrients in smaller, freshly moulted larvae. Moreover, larvae reduce or stop feeding before each moult (Lawton 1971). Our result thus demonstrates the necessity of higher energy intake at the start of each instar. Surprisingly, we did not find decreasing predation rates with body size within F-0 instar. While the final stages of the F-2 and F-1 instar are difficult to detect, late F-0 larvae are easily recognized (swollen wing pads, changes to head morphology) and invariably stop feeding (Corbet 1999). They were thus not used in the experiment, which may explain the lack of decrease in predation rates with body mass within F-0 larvae.

Comparison of feeding and metabolic rates

Metabolic rates sometimes increase faster with temperature than feeding rates (Vucic-Pestic et al. 2011; Iles 2014) which can lead to less energetic efficiency of predator at higher temperature. Metabolic demands may therefore exceed ingestion rates and cause starvation of predators at high temperature (Petchey et al. 1999; Rall et al. 2010). In agreement with these studies, we found higher effect of temperature on metabolic rates than on feeding rates across all instars of *Aeshna* included in this study. Moreover, the dragonflies (except possibly the largest F-0 larvae at the highest temperature) were not food limited in our experiment. This shows that these dragonflies can be negatively impacted by increased temperatures.

Prey perspective

Not every predator attack is successful and sometimes predators reject caught prey. Both types of events can cause lethal injuries of the prey that contribute to prey mortality

but not to the energetic gain of the predators (Johnson, Akre & Crowley 1975; Corbet 1999). The most common injuries of uneaten tadpoles caused by dragonfly larvae in our experiment were tattered or missing tail fins, which are necessary for tadpole movement and always lead to death of the tadpole. Similar to predation rates, total mortality of tadpoles increased with temperature and dragonfly instar. Moreover, within each instar, smaller predators caused higher total prey mortality as the older larvae were feeding less.

Several studies demonstrated different thermal dependence of growth and development (Forster & Hirst 2012; Zuo et al. 2012) and growth and metabolic rate (Person-Le Ruyet et al. 2004; Chopelet, Blier & Dufresne 2008) of ectotherms. *Bufo bufo* tadpoles and other larvae of amphibians can accelerate development at higher temperatures to leave early the aquatic environment, but at the cost of smaller size at metamorphosis (Brady & Griffiths 2000). Here, we found that metabolic rates increased with temperature but the relatively short duration of the experiment did not allow us to assess the concurrent temperature-dependent changes in growth and development. Further experiments can shed more light on the joint thermal dependence of metabolic, growth and developmental rates in tadpoles.

Conclusions

Temperature increases metabolism and intensity of predation (Sentis et al. 2012; Sentis et al. 2015). In this study, we showed that warming affects biological rates of both predator and prey and that these changes impact interaction strengths. We also show that the feeding and metabolic rates can change dramatically during ontogeny, which might lead to short-term but potentially serious consequences for individual fitness. Thus, our results can help refine the prediction of the effects of climate change on ecological communities.

On long time scales, intensity of predation is further affected by growth rates and abundance of prey (Berlow et al. 2009). Our experiments ran for a short time and we tested the effect of feeding and metabolic rates of predator on predation regardless of numerical response in predator and prey abundance. To fully predict the impact of increased temperature on interaction strengths, additional studies investigating long-term interactions from both predator and prey perspective are needed.

Moreover, the effect of multiple stressors can change the outcome in comparison to studies based on single stressors. For example, tadpoles of many amphibian species accelerate their development in response to desiccation stimuli (e.g., decreasing volume of water or increasing density of tadpoles) as an impact of warming (Rudolf & Rodel 2007) and in response to predation risk (Stav, Kotler & Blaustein 2007), but their combined effects are little known.

Authors' Contributions

DSB and DM conceived the ideas and designed methodology; MD collected the data; DSB and DM analysed the data; DM and DSB wrote the manuscript.

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Figures

Fig. 1: Dependence of predator mass gains on number of eaten tadpoles. Solid lines = mean model prediction, dashed lines = 95% prediction interval, symbols = individual observations.

Fig. 2: Effect of temperature and body mass of dragonfly larvae on probability of predation after 24 hours. Panels show individual dragonfly instars. Solid lines = mean model prediction, dashed lines = 95% CI, symbols = individual observations; blue square = 15°C, green triangle = 20°C, red circle = 25°C.

Fig. 3: Effect of temperature and body mass of dragonfly larvae on total mortality of tadpoles after 24 hours. Panels, lines, symbols and colour coding as in Fig. 2.

Fig. 4: Effect of temperature and body mass on metabolic rate of dragonfly larvae and tadpoles. Lines and colour coding as in Fig. 2; symbol shapes: circle = tadpole, triangle = F-2 dragonfly instar, square = F-1 dragonfly instar, cross = F-0 dragonfly instar.

Figure 1

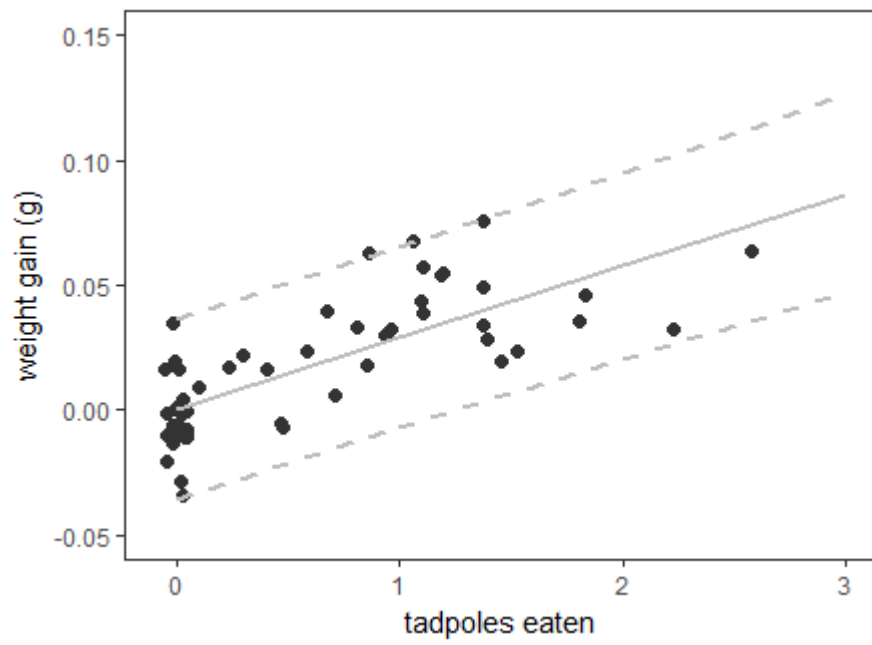


Figure 2

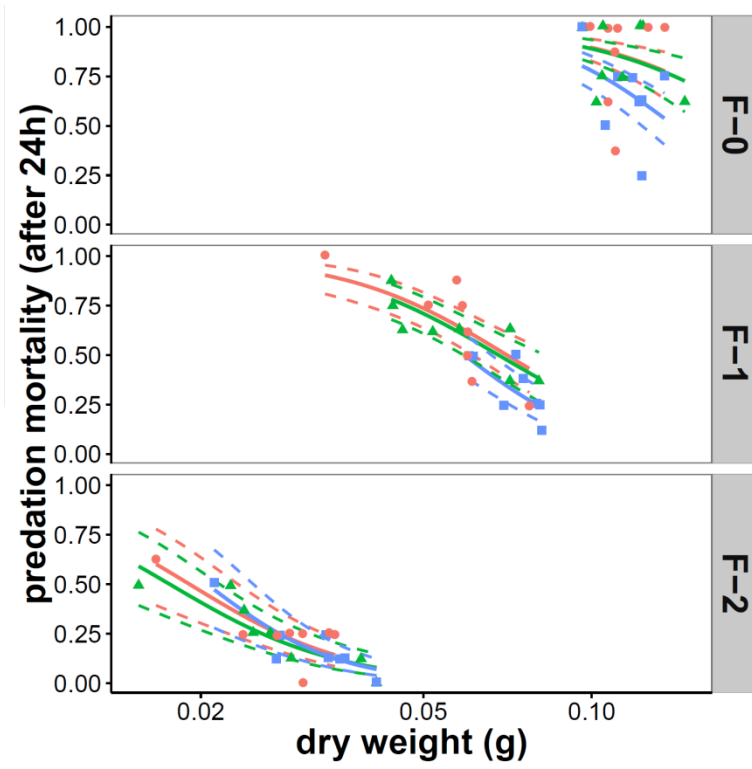


Figure 3

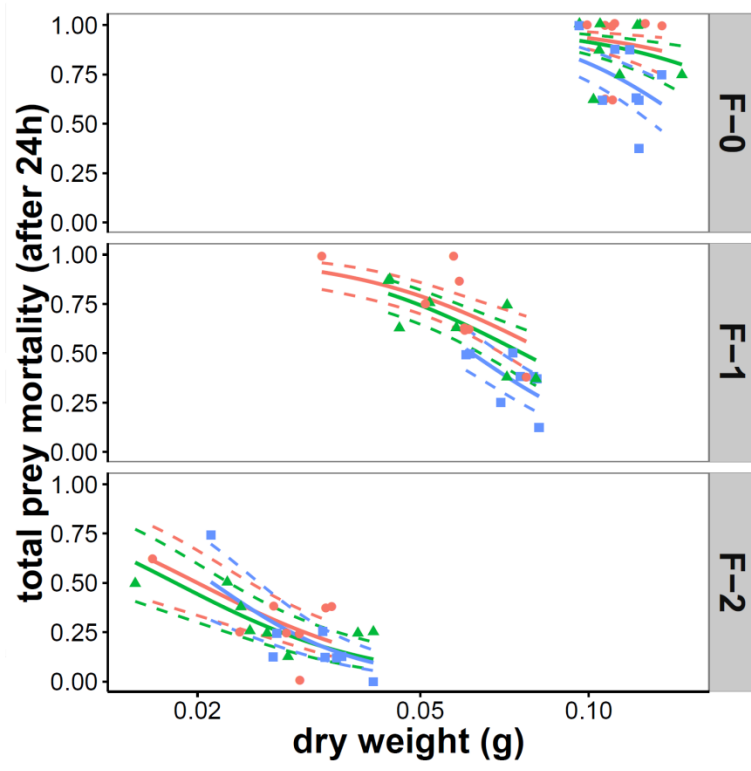
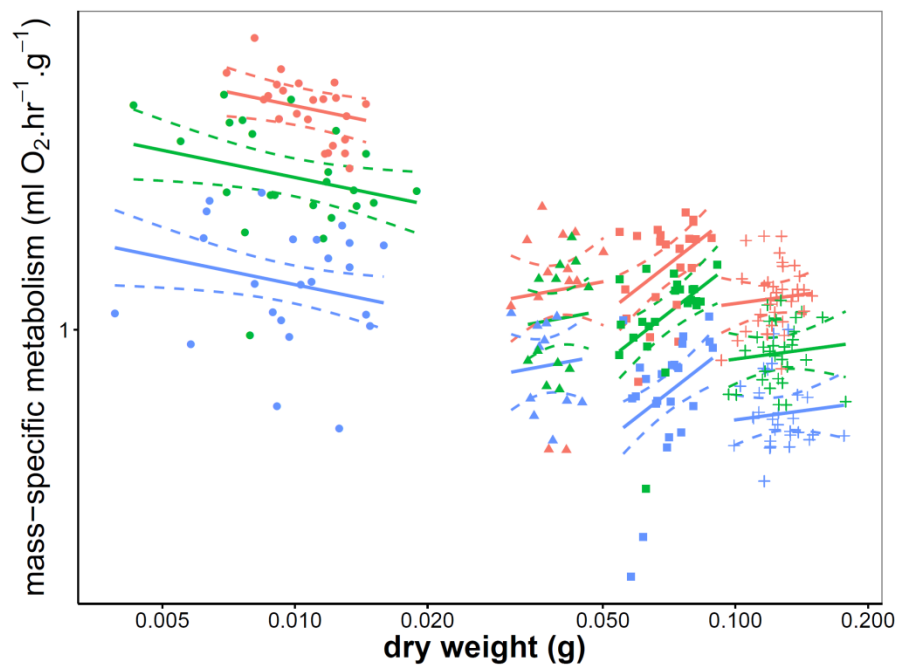


Figure 4



Tables

Table 1: ANOVA table summarizing the effects of instar, temperature and predator dry weight w on the proportion of tadpoles eaten by the dragonfly larvae after 24 hours of the experiment based on the results of the most parsimonious binomial GLM.

Effect	Df	Residual df	Deviance	P
Instar	2	69	121.7	< 0.0001
Temperature	2	67	22.3	< 0.0001
Log(w)	1	66	34.8	< 0.0001
Temperature x Log(w)	2	64	4.2	0.12
Residuals			78.8	

Table 2: ANOVA table summarizing the effects of instar, temperature and predator dry weight w on total mortality of tadpoles after 24 hours of the experiment based on the results of the most parsimonious binomial GLM.

Effect	Df	Residual df	Deviance	P
Instar	2	69	126.6	< 0.0001
Temperature	2	67	26.0	< 0.0001
Log(w)	1	66	27.0	< 0.0001
Temperature x Log(w)	2	64	5.5	0.06
Residuals			78.5	

Table 3: ANOVA table summarizing the effects of instar, temperature and predator dry weight w on respiration rates of tadpoles and dragonfly larvae.

Effect	Df	F	P
<i>Bufo</i>			
Temperature	2	86.1	< 0.0001
Log(w)	1	43.5	< 0.0001
Residuals	65		
<i>Aeshna</i>			
Instar	2	198.6	< 0.0001
Temperature	2	106.8	< 0.0001
Log(w)	1	88.3	< 0.0001
Instar x Log(w)	2	3.1	0.05
Residuals	192		

Table 4: Coefficients of the most parsimonious model describing the effects of temperature and dry weight w on respiration rates of tadpoles and dragonflies. Intercept respectively denotes the predicted oxygen consumption (as $\log_{10} \text{O}_2 \text{ ml.h}^{-1}$) of a 1 g tadpole or F-2 dragonfly larva (dry weight) at 25° C. $\text{Log}(w)$ denote the respective size allometry exponents; temperatures denote the respective differences from 25°C; F-1 and F-0 denote differences from F-2.

Variable	Estimate \pm SE	<i>t</i>	P
<i>Bufo</i>			
(Intercept)	0.11 \pm 0.23	0.48	0.64
Temperature (20°C)	-0.18 \pm 0.04	-4.82	< 0.0001
Temperature (15°C)	-0.46 \pm 0.04	-12.01	< 0.0001
Log(w)	0.77 \pm 0.12	6.60	< 0.0001
<i>Aeshna</i>			
(Intercept)	0.17 \pm 0.58	0.29	0.77
F-1	0.99 \pm 0.64	1.54	0.12
F-0	0.03 \pm 0.62	0.05	0.96
Temperature (20°C)	-0.12 \pm 0.02	-6.25	< 0.0001
Temperature (15°C)	-0.29 \pm 0.02	-14.46	< 0.0001
Log(w)	1.02 \pm 0.41	2.46	0.015
F-1 x Log(w)	0.86 \pm 0.47	1.81	0.07
F-0 x Log(w)	0.12 \pm 0.48	0.26	0.80

Appendix

Table S1: Number of replicates in Experiment 2 (*Effect of temperature and body size on predator and prey metabolic rates*).

Instar	15°C	20°C	25°C
F-2	11	12	13
F-1	24	23	22
F-0	30	30	35
Tadpole	23	24	23